Powerful fish in poor environments: Energetic trade-offs drive distribution and abundance in an extremophile forest-dwelling fish

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Contents

Frontispiece: An adult brown mudfish (*Neochanna apoda*) swimming in an artificial aquarium with mossy vegetation and detritus typical of its forest pool habitat. Photo credit: Angus McIntosh.

Abstract

For many species, distribution and abundance is driven by a trade-off between abiotic and biotic stress tolerance (i.e. physical stress versus competition or predation stress). This trade-off may be caused by metabolic rate differences in species such that slow metabolic rates increase abiotic tolerance but decrease biotic tolerance. I investigated how metabolic rate differences were responsible for an abiotic-biotic tolerance trade-off in brown mudfish (*Neochanna apoda*) and banded kokopu (*Galaxias fasciatus*), that drives the allopatric distribution of these fish in podocarp swamp-forest pools. Brown mudfish and banded kokopu distribution across 65 forest pools in Saltwater forest, Westland National Park, New Zealand was almost completely allopatric. Mudfish were restricted to pools with extreme abiotic stress including hypoxia, acidity and droughts because of kokopu predation in benign pools. This meant the mudfish realised niche was only a small fraction of their large fundamental niche, which was the largest out of sixteen freshwater fish species surveyed in South Island West Coast habitats. Thus mudfish had a large fundamental to realised niche ratio because of strong physiological stress tolerance but poor biotic stress tolerance compared to other fish. A low metabolic capacity in mudfish compared to kokopu in terms of resting and maximum metabolic rates and aerobic scope explained the strong mudfish tolerance to extreme abiotic stress, but also their sensitivity to biotic stress by more powerful kokopu in benign pools, and hence their allopatric distribution with kokopu. Despite being restricted to extreme physical stress, mudfish populations were, in fact, more dense than those of kokopu, because of low individual mudfish resting metabolic rates, which would cause resources to be divided over more individuals. Distribution and abundance in mudfish and kokopu were therefore driven by an abiotic-biotic tolerance trade-off caused by a physiological trade-off between having slow or fast metabolic rates, respectively. The

negative relationship between species resting metabolic rates and their tolerance to abiotic stress provides a way of estimating the impact of human induced environmental change that can either increase or decrease habitat harshness. Thus species with low metabolic rates, like mudfish, will be negatively affected by human induced environmental change that removes abiotic habitat stress and replaces it with benign conditions. My evidence shows that extreme stressors provide a protective habitat supporting high mudfish biomass with significant conservation value that should be maintained for the long-term persistence of mudfish populations.

Chapter One:

General Introduction

Introduction

Understanding the drivers of distribution and abundance (D&A) is a vital theme in predictive ecology (Guisan & Thuiller 2005). Distribution and abundance can be affected by both intrinsic species traits and environmental conditions (McGill et al. 2006), both of which are highly variable, making it unlikely that general ecological laws can be applied to predict D&A at small local scales (Lawton 1999). Consequently, some ecologists have encouraged the search for ecological generalities at global macro-ecological scales, where ecological responses are averaged and local deviations are mostly considered as a nuisance residual (Lawton 1999). Although this approach has produced many generally applicable insights (Brown & Maurer 1989; Brown, Stevens & Kaufman 1996; Hawkins *et al.* 2003), ecological management is often applied to specific species or locations where residual variation may be more, or at least as, important as a macro-ecological prediction (Simberloff 1995). Moreover, understanding why such species or locations deviate from macro-ecological patterns may not only improve D&A predictions, and thus environmental management at local scales, but may also enrich our understanding of the fundamental laws generating the macro-ecological patterns themselves.

The metabolic theory of ecology (MTE) is a macro-ecological theory that has been the focus of intense interest in recent decades (West, Brown & Enquist 1997; West, Brown & Enquist 1999; Gillooly *et al.* 2001; Brown *et al.* 2004). Metabolic theory predicts ¼ power scaling of ecological phenomena with individual or species mass because of the fundamental ¾ power scaling of resting metabolic rates (RMR) with mass (Brown et al. 2004). For example, because RMR increases with an individual's mass with a slope of 0.75, maximum

population density should decline with the average mass of individuals in a population with a slope of –0.75 (Damuth 1981; Brown *et al.* 2004). This reasoning invokes an additional fundamental concept, that maximum population carrying capacity (*C*), all else being equal, should equal energy availability (*E*) divided by the per-capita energy consumption rate (P_c) (i.e. $C = E / P_c$) (Damuth 1981; Carbone & Pettorelli 2009). Consequently, as mass increases, *E* is divided by an increasingly larger number (i.e. $P_c = \text{mass}^{0.75}$), and therefore, *C* must decline (i.e. $C = \text{mass}^{-0.75}$) (Damuth 1981; Brown *et al.* 2004). While this metabolic principle has had some support at large ecological scales (Damuth 1981; Nee et al. 1991), there is still large residual variation in its predictions for specific species and locations (Blackburn & Gaston 1999). Moreover, as body size range declines to that which is more likely at local scales, this residual variation increases relative to that which is explained by body size (Isaac, Storch & Carbone 2013), and the slope of the size-density relationship (SDR) can fluctuate greatly (Isaac, Storch & Carbone 2011). Consequently, the applicability of individual or species mass as a universal predictor of density may be of limited use at small scales, where location and species-specific knowledge may be more predictive.

One of the most common criticisms levelled at MTE focuses on the variation in the metabolic mass scaling exponents that can exist both within and between species (Bokma 2004; Glazier 2005). Exponents can fluctuate inter-specifically from greater than 1 to nearly 0, across several taxa, and can vary greatly within species due to individual growth rate differences (Bertalanffy 1951; Glazier 2005; Czarnołęski *et al.* 2008). Only when species-specific exponents are averaged across taxa does the exponent approach 0.75, and consequently, the universal metabolic scaling law is only useful at macro-ecological scales (Isaac & Carbone 2010). Moreover, Isaac et al. (2011) point out this inter-taxon variation fails to account for taxon-specific slope differences in size-density relationships in animals (Isaac, Storch & Carbone 2011). This challenges the validity of MTE density predictions for

animals at both large and local ecological scales, because the metabolic foundations upon which MTE rests involves sub-organism mechanics (West, Brown & Enquist 1997; West, Brown & Enquist 1999), and thus should apply, at least, at between-taxon scales.

There are also many other factors that scale allometrically with mass (Woodward et al. 2005), which may confound the effect of metabolism on SDR slopes. For example, as organisms increase in mass, they also gain access to greater amounts of food due to the relaxation of gape size limitations (King 2002). Consequently, an increase in food available to larger organisms could offset the costs of increased consumption rates thus altering the slope of SDRs (Begon, Firbank & Wall 1986; Steingrímsson & Grant 1999), even if the total food available to the whole population remains constant. Using mass-independent metabolic rate as a predictor of density avoids confounding allometric factors and may therefore be a better way of testing the fundamental effects of metabolic variation on density as embodied in the MTE (Blackburn, Lawton & Gregory 1996; Blackburn & Gaston 1999). However, very few studies have attempted this (Blackburn, Lawton & Gregory 1996; King 2010).

More recently McGill and colleagues (2006) argued that understanding how functional traits vary along environmental gradients will enable better generalisation of ecological principles at any ecological scale. If such traits are linked to species performance (i.e. population density), then a functional-traits-on-gradients approach may allow the mapping of species performance geographically along abiotic contours (McGill et al. 2006). Thus the fundamental niche of a species may be estimated allowing accurate species distribution predictions based on traits (McGill et al. 2006). Such traits could also estimate species' realised distributions, based on how they predict biotic performance (i.e. the ability to compete, capture prey or escape predation) (McGill et al. 2006). Thus traits that increased performance in stressful abiotic conditions (i.e. increased fundamental niche), but simultaneously decreased biotic performance (i.e. realised niche), may cause a species to

have a realised distribution that is much smaller than its fundamental niche. According to MTE, RMR is the fundamental functional trait determining species performance in terms of growth, reproduction, species interactions or by determining population growth and density (Brown et al. 2004). Combining MTE with the functional-traits-on-gradients approach that uses mass-independent metabolic variation between species may therefore enable predictions of species D&A along both small and large geographic scales, allowing MTE to be more locally relevant and useful for management.

Habitat Templet (HTT), and Maximum Power (MPT) theories provide suitable frameworks for predicting species performance along abiotic and biotic stress gradients based on metabolism because together they define the abiotic-biotic context within which a fast or slow metabolic rate may evolve in a species (Lotka 1922; Southwood 1977; Greenslade 1983; Southwood 1988). Maximum power theory predicts that biological systems will organise to maximise energy flux within environmental constraints (Lotka 1922; Odum & Pinkerton 1955), a concept grounded in successional theory (Odum 1969). Thus MPT provides an energetic definition of fitness by linking consumption rates with life-history traits such as growth rates and reproductive output (Brown, Marquet & Taper 1993). While life-history parameters and inter-specific dominance are often positively correlated with consumption rates (DeLong 2008; Biro & Stamps 2010), the relationships are heavily context-dependent, implying a trade-off between fast versus slow (fast-slow) metabolism determined by the environment (Burton et al. 2011). Understanding what environmental contexts drive this fast versus slow metabolism should allow MTE mapping to local environmental conditions. The environmental context for such a fast-slow metabolic trade-off is provided by HTT theory, which predicts that life history traits (e.g. growth and reproductive rates) will correlate positively with biotic stress (e.g. competition/predation) and negatively with environmental stress (Southwood 1977; Greenslade 1983; Southwood 1988).

Thus an abiotic-biotic tolerance trade-off is the primary force selecting for fast versus slow life-histories under HTT (Figure 1a).

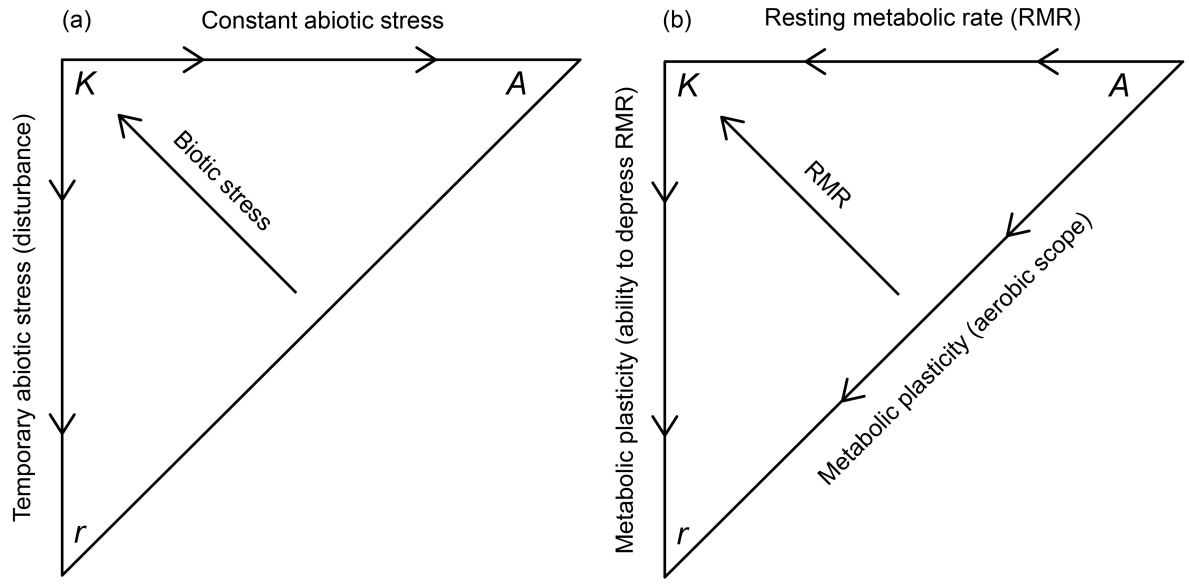


Figure 1: a) The Southwood-Greenslade habitat templet, adapted from Southwood (1988) to highlight the distinction between, temporary and consistent abiotic stress, and biotic stress, which increases as temporary and constant abiotic stress decrease. Individual and population growth rates and reproductive output decreases from *K*- to *A*-selected species (i.e. fast versus slow life-histories) as abiotic conditions become constantly more stressful (i.e. mesic to arid), and biotic stress (e.g. competition) declines. Temporally fast life-histories evolve (i.e. those traditionally called *r*-selected) where conditions fluctuate between environmentally stressful and benign conditions so as to capitalise on short favourable growth periods. Because growth and reproduction requires energy, these life-history strategies may translate into the metabolic traits in **(b)**, with low mass-specific RMR (resting metabolic rates) for *A*-selected species living in constant energy stress, and high RMR for *K*-selected species living in competition/predation-intense habitats with high species richness. High metabolic plasticity (i.e. aerobic scope or metabolic depression) may occur in *r*-selected species allowing them to capitalise on benign periods for rapid growth (high aerobic scope), but tolerate periods of abiotic stress by temporally depressing RMR. *K*-selected species may also have a high aerobic scope to enhance foraging and predation capacity, but are predicted to lack metabolic depression ability because of the lack of temporary stress.

Habitat templet theory defines environmental stress primarily as low habitat productivity, however, this may also include any abiotic factor that reduces an organisms capacity to acquire or use energy to maintain homeostasis regardless of the availability of habitat energy (Southwood 1988). For instance, hypoxia limits redox potential for oxidative phosphorylation leading to inefficient anaerobic substrate consumption, while the increased thermodynamic stability of enzymes at low temperatures reduce the rate at which enzymes can consume ATP (Hochachka 1986; Hochachka 1988). Environmental stress can also be permanent or temporary, for instance, drought temporarily induces aquatic-hypoxia, desiccation and starvation (Bond, Lake & Arthington 2008; Urbina & Glover 2013). Because these are all ultimately forms of energy stress, a low RMR is likely to increase organism tolerance to multiple stressors (Figure 1b) (Hochachka 1986; Hochachka 1988). However, whether low metabolism is fixed or flexible may depend on the temporal nature of abiotic stressors. For instance, species subjected to temporary stress punctuated by benign periods may be capable of increasing their metabolism to capitalise on favourable growth periods (Figure 1b) (Welborn, Skelly & Werner 1996). Because these predictions are based on differences in local conditions, they may be useful frameworks for adapting MTE to specific localities. They also have the added power of explaining how metabolic variation may affect species distribution, through the opposing way in which RMR may effect abiotic (i.e. fundamental niche) and biotic stress tolerance (i.e. realised), and thus how species fundamental niche and realised niches are determined.

A functional traits-on-gradients approach involving MTE, HTT and MPT will enhance prediction of species D&A in several ways. Firstly, by understanding the fundamental abiotic-biotic tolerance trade-off in terms of a fast-slow metabolic continuum, we may be able to accurately predict species fundamental and realised niche and thus distribution along abiotic contours. Secondly, understanding how and why metabolism varies

along abiotic and biotic gradients may allow local adaptation of MTE and thus precise predictions of how ecological function (e.g. population density) varies along such gradients. MTE proponents argue that metabolic rates are the DNA of ecology, ultimately predicting that all species are equal in function when compared on a gradient of metabolic rates (Sibly, Brown & Kodric-Brown 2012). Consequently, understanding how metabolism varies inter-specifically along abiotic and biotic gradients may diminish much of the variability in ecological responses caused by species identity and environmental factors, allowing fundamental macro-ecological concepts to be locally relevant.

The brown mudfish (*Neochanna apoda*) is an excellent model organism with which to test a functional-traits-on-gradients framework involving MTE, MPT and HTT theories because they are one of the most abiotic stress-tolerant fish known. Brown mudfish are a threatened freshwater fish endemic to the peat swamp podocarp forests of New Zealand. They inhabit shallow pools that have extremely large temperature ranges (<1 - 25°C), moderate to low pH (pH 3.5 – 8.0), can be nearly fully anoxic (<1.0 mg O_2 L^{-1}) and dry completely, frequently, and unpredictably for weeks at a time (McDowall 2006), any one of which is lethal to most fish (Figure 2a - d). This tolerance may have been driven by an abiotic-biotic tolerance trade-off as mudfish rarely co-occur with other galaxiid fish (Eldon 1968). In particular they rarely co-occur with the banded kokopu (*Galaxias fasciatus*) (Waters & McDowall 2005), despite kokopu inhabiting similar, but more benign, swampy pools and streams (Eldon 1968).

Figure 2: Photomontage of brown mudfish habitats from Saltwater forest (SWF), Westland National Park, New Zealand, illustrating the range of environmentally stressful conditions brown mudfish experience. Images **(a)** and **(b)** show the contrast in hydrological conditions during a drought and inundated period respectively, for the same pool. Most pools dry up at a rate of approximately 10 – 20 mm d^{-1} making shallow pools particularly drought-prone. Image **(c)** is an example the most common type of mudfish habitat in SWF: a pool that has formed after the uprooting of a large podocarp tree, with the distinctive root plate shown vertically. Image **(d)** is an aquatic view from a mudfish pool (lower half), with the forest canopy overhead (top half). The hypoxic, acidic, tannin stained, brown water is formed from the biological breakdown of forest detritus that has built up on the benthos, which ultimately decomposes to form a deep peat layer underneath. Photo credits: Richard White: (a) and (b); and Angus McIntosh: (c) and (d).

This trade-off would have once been a highly successful strategy due to the extensive area historically covered by temporary forested wetlands along New Zealand's low-lying West Coast (James & Norton 2002), making it one of the most abundant habitat types in the region. However, this situation has reversed due to extensive deforestation followed, in most cases, by wetland drainage into pasture. Thus mudfish are restricted to a few pockets of habitat where extreme conditions still prevail, which has contributed to the declining and vulnerable state of brown mudfish (McDowall 2006). Consequently, mudfish are another example of a freshwater fish threatened with extinction due to destruction of peat-swamp-forests (Giam et al. 2012). This represents a maximum scope of potential realised niche loss, as deforestation removes the detrital inputs that contributes to the hypoxia and acidity, and affects temperature regimes in the wetland pools. Meanwhile, wetland drainage removes pool ephemerality, leaving permanent drain ditches that are habitable by many other fish. Human land use is expected to intensify in such ecosystems (Giam et al. 2012) making it important to understand what extreme abiotic conditions are important dimensions of the mudfish realised niche, and how this interacts with physiology and biotic factors.

Thesis layout

Species niche is often considered as an *n*-dimensional hypervolume (Hutchinson 1957) such that it is impossible to investigate all possible important factors. Thus McGill and colleagues (2006) suggest a functional-traits-on-gradients approach should first prioritise environmental and biotic factors that determine fundamental and realised niche. Accordingly, in Chapter Two I focussed on prioritising the abiotic and biotic factors that determined the realised distribution of the brown mudfish and banded kokopu in the Saltwater forest, in Westland New Zealand. I selected a series of abiotic stress, habitat heterogeneity and biotic factors (e.g. presence/absence of kokopu and other in/vertebrates) that may determine the

abiotic-biotic tolerance trade-off in mudfish and kokopu and hence drive their distribution. I hypothesised mudfish would have a small realised distribution restricted to environmental extremes because of the presence of kokopu in benign conditions. Thus mudfish distribution would be driven by an abiotic-biotic tolerance trade-off. My goal was to determine which abiotic extremes were important drivers of this realised distribution.

In Chapter Three, I asked if a slow versus fast metabolic trade-off between kokopu and mudfish may be driving the abiotic-biotic tolerance trade-off discovered in Chapter Two. I measured resting metabolic rates (RMR), maximum metabolic rates (MMR), and aerobic scope (AS) over a 15-30 g fish mass range for both mudfish and kokopu. I hypothesised that a low RMR, MMR and AS would increase the mudfish tolerance to the abiotic stressors identified in Chapter Two, but would also reduce their tolerance to competition and predation by banded kokopu in benign conditions such that slow versus fast metabolic differences would drive the abiotic-biotic tolerance trade-off in mudfish and banded kokopu, and thus drive their distribution. I also conducted a population size survey of 39 mudfish forest pools, and 25 kokopu forest pools, to investigate whether the metabolic differences between mudfish and kokopu could explain the differences in population densities between these species. As per the MTE, I predicted that mudfish would reach significantly higher population densities, despite being a smaller fish, because of significantly lower RMR. Thus by explaining species differences in metabolism as a function of abiotic and biotic stress, I hoped to adapt MTE to local mudfish and kokopu populations.

In Chapter Four I synthesise and explore the generality of my research in Chapters Two and Three, by comparing my findings with data collected on other New Zealand native and introduced freshwater fish. Finally, I discuss how my results might apply towards conservation management of freshwater organisms in the context of environmental change in New Zealand, particularly in West Coast freshwaters on the South Island.

This thesis is written as a series of stand-alone papers that will be submitted for publication. Angus McIntosh, Chris Glover and Pete McHugh will be co-authors on these papers, in addition to myself, and their contributions are acknowledged in the acknowledgements section of this thesis, along with any other contributions from other people.

Chapter Two

The abiotic-biotic stress tolerance trade-off in an extremophile forest-dwelling fish: the habitat portfolio effect on distribution

Abstract

The loss of physically extreme environments due to increasing human land use change is threat to species that inhabit extreme environments. These extremophiles are highly vulnerable to extinction because of a severely restricted realised niche associated with a trade-off between abiotic and biotic stress tolerance. I examined whether multiple abiotic stress tolerances in an extremophile forest-pond-dwelling fish, the endangered brown mudfish (*Neochanna apoda*), could increase their realised niche by providing refuge from their most common predator, the banded kokopu (*Galaxias fasciatus*). Fish distributions were surveyed in 65 forest streams and pools, which varied in hypoxia, acidity and hydroperiod. Mudfish distribution was extremely patchy, and almost completely allopatric with kokopu. Allopatry was driven mainly by pool hydroperiod; mudfish occupied 88 percent of temporary pools due to their tolerance of habitat drying, whereas kokopu were absent from temporary pools. Within permanent pools, mudfish occurrence was negatively affected by increasing pool oxygen and pH, whereas kokopu were positively affected by less stressful oxygen and pH conditions. The deviance explained by each abiotic stressor was autocorrelated with kokopu presence but not with other stressors, suggesting that each abiotic stressor offered complementary refuge for mudfish from kokopu predation. Consequently, the mudfish realised niche was much larger than if only one abiotic stress was considered. Mudfish have a much larger fundamental niche than the observed realised niche, thus species interactions are responsible for generating a large mudfish fundamental-realised niche ratio. This indicates species interactions should be given priority when explaining the distributions of

extremophiles and their management should focus on how crucial extremes of their realised niche are altered by environmental change.

Introduction

The loss of physically extreme environments due to increasing habitat modification by humans is a major concern for global biodiversity (Skole & Tucker 1993; Brinson & Malvárez 2002; Peck 2005; Giam *et al.* 2012). Species that survive extreme environments (extremophiles) require specialised physiological adaptations that are frequently traded off with competitive or anti-predatory abilities (Southwood 1988). Consequently, extremophiles are often limited to harsh environments because they are ill-equipped to tolerate the biotic forces structuring communities in benign environments (Holway, Suarez & Case 2002; Alcaraz, Bisazza & García-Berthou 2008; Krassoi *et al.* 2008). In some cases, particularly for freshwater fish, this abiotic-biotic tolerance trade-off is linked to allopatric distributions along abiotic gradients, often allowing native species to avoid the negative influence of invasives (McIntosh 2000; Taniguchi & Nakano 2000; Rieman, Peterson & Myers 2006). Thus, the abiotic-biotic trade-off has far-reaching implications for changing species distributions associated with many facets of human-induced environmental change (Krassoi et al. 2008). In particular, the trade-off implies that extremophiles will be highly sensitive to habitat modification, which often involves a change to a more benign state supportive of humanity (Giam et al. 2012). Moreover, extremophile distributions are potentially driven strongly by biotic interactions in benign conditions and hence indirectly by abiotic factors. This complication, and the extent of human-induced environmental change means better knowledge of the interactive effects of biotic and abiotic forces structuring communities is needed (Davis et al. 1998).

The degree to which extremophiles are co-tolerant to multiple environmental stressors

is likely a key factor mediating their resistance to environmental change (Vinebrooke et al. 2004). Species that are tolerant of extreme stress are likely to have a large fundamental niche so could potentially be present at both benign and stressful ends of abiotic gradients. However, the abiotic-biotic tolerance trade-off means these species often show severely reduced realised niches due to extirpation by dominant competitors and predators in benign environments, resulting in large fundamental-realised niche ratios (Vetaas 2002). A restricted realised niche may increase a species' sensitivity to habitat modification if they are limited in alternative habitat (Purvis et al. 2000). For example, this could explain why acidophilic fish in peat swamp forests are the most vulnerable to extinction by anthropogenic habitat modification in South East Asia (Giam et al. 2012). However, if each stressor offers complementary refuge from other dominant species, the size of the realised niche may increase depending on the number of stressors an extremophile is tolerant to. Thus extremophile populations could be more resistant to changing environments because of the availability of alternative habitats (Purvis et al. 2000). Quantifying if and how multiple environmental extremes contribute to the realised niche of extremophile species will therefore highlight the mechanisms that will reliably support extremophile populations.

I investigated how multiple extreme conditions contribute to the realised niche of the brown mudfish (*Neochanna apoda*), a threatened freshwater fish (McDowall 2006) endemic to New Zealand with one of the widest environmental tolerances known. Brown mudfish inhabit stagnant, shallow, peat-swamp-forest pools that have extremely large temperature ranges (<1 - 25°C), moderate to low pH (pH 3.5 – 8.0), can be nearly fully anoxic (<1.0 mg O_2 L^{-1}) and dry completely, frequently, and unpredictably for months at a time (McDowall 2006). Any one of these stressors is usually lethal to most fish yet mudfish experience them frequently and often simultaneously. In fact, this fish is often accidentally dug up from peaty soils well away from any standing water sources (Eldon 1968). I hypothesised that mudfish

abiotic tolerance has been driven by an abiotic-biotic tolerance trade-off as mudfish rarely co-occur with other galaxiid fish, including the most likely common mudfish ancestor, the banded kokopu (*Galaxias fasciatus*) (Waters & McDowall 2005), which inhabits swampy pools and streams similar to brown mudfish habitat (Eldon 1968).

This trade-off may have once been a highly successful strategy due to the extensive area historically covered by temporary forested wetlands along New Zealand's low-lying West Coast (James & Norton 2002), making it one of the most abundant habitat types in the region. This situation has reversed due to extensive deforestation followed, in most cases, by wetland drainage into pasture, which has contributed to the declining and vulnerable state of brown mudfish (McDowall 2006). Consequently, mudfish are another example of a freshwater fish threatened with extinction due to destruction of peat-swamp-forests (Giam et al. 2012). This represents a maximum scope of potential realised niche loss, as deforestation removes the detrital inputs that contributes to the hypoxia and acidity, and affects temperature regimes in the wetland pools, whilst drainage removes the temporary periodicity of pools leaving permanent drain ditches that are habitable by many other fish. Human land use is expected to intensify in such ecosystems (Giam et al. 2012) making it important to understand how multiple stressors contribute to the realised niche of extremophiles such as the brown mudfish.

I investigated how multiple environmental stressors controlled the allopatric distribution of brown mudfish and banded kokopu in the Saltwater Forest, one of the few remaining temperate swamp-forest remnants in New Zealand. The relative importance of physiological stress factors including drought, acidity, oxygen and temperature was compared with variables describing within-habitat heterogeneity (e.g. submerged woody debris). Within-habitat heterogeneity can provide refugia for species sensitive to predation and hence allow species co-existence or explain allopatry (Everett & Ruiz 1993). However, conditions

that are highly stressful can be a powerful selective force determining species occupancy (Chase 2007). Thus I hypothesised that physiological stress parameters would explain more deviance in mudfish occupancy than within habitat heterogeneity. I predicted that drought would provide the strongest delineation of mudfish and kokopu distribution due to the significant stress this places on freshwater fish. However, the combination of oxygen, temperature and acidity stress could promote further allopatry in permanent pools due to their likely negative effect on kokopu. If these stresses acted complementarily, then multiple extremes would create a portfolio effect, whereby the absence of one stressor could be replaced by another, thus greatly increasing mudfish realised niche.

Methods

Study area and design

The Saltwater forest, located within Westland National Park, on the West Coast of the South Island, New Zealand (43°06'S, 170°23'E) is a 9000 ha temperate peat-swamp-rainforest dominated by rimu (*Dacrydium cupressinum*), with sections of kahikatea (*Dacrycarpus dacrydioides*) (Rogers 1999). A slight gradient prevails towards the coast, which, combined with the poorly drained peaty soils and high annual rainfall of 3742 mm (Rogers 1999) results in a mossy, waterlogged, forest floor dotted with numerous small pools. The pools may be temporary or permanent and are usually the remains of tree fall excavations and other depressions caused by tree senescence or wind throw damage. Small channels permeate the forest, many of which have intermittent flow.

Sampling was timed with significant weather changes to capture the maximum variability in hydrological conditions and fish population states, and study locations were distributed along the elevation gradient to capture a wide range of drainage conditions. I sampled from 65 forest pools and channels on two separate occasions; a dry period (6 to 11

December 2010), which followed a severe one-month drought when regional water restrictions were in place, and a wet period (29 December 2010 to 2 January 2011), which followed two and a half weeks of heavy rain. This ensured that contrasting dry and wet periods in mudfish habitat could be described, and allowed for identification of temporary pool habitats. Seven 100 x 10 m transects were marked out during the dry period with at least one transect located on each contour line in the forest from 100 to <20 m altitude towards the coast. Transect positions along a contour line were chosen randomly by selecting a grid square from all possible squares containing a road/track intersecting a given contour line. Transects were placed perpendicular to the road/tracks, starting approximately 10 m into the forest. All standing waters, including channels and pools, were sampled within these transects averaging approximately 10 pools per transect. Most pools sampled in the dry period were re-sampled in the wet period, including any new pools that were previously dry, however transects 5 and 6 were not revisited for logistical reasons.

Fish and habitat sampling

Fish were sampled using un-baited 3.12 mm mesh Gee minnow traps (420 mm L x 220 mm W) set for 12 h overnight. An initial experiment was conducted to test for the efficacy of using marmite bait (Eldon 1992) to catch mudfish, whereby fifteen baited and fifteen un-baited traps were set for 24 h overnight in eleven separate pools, and their catch was recorded. A poisson generalised linear mixed effects model was used to test for differences in mudfish catch per unit effort (CPUE) between baited, and un-baited traps, which revealed no significant effect of the bait ($F_{1,17}$ = -0.09, P < 0.93). Traps were spaced approximately 2 m apart in larger habitats and a small space above the water surface was provided in the trap to allow fish access to surface air. Pools that were not large enough to fit a trap had to be excavated with a small shovel; however, this was only done where pools

were only marginally too small. Upon capture, mudfish were anaesthetised with a 0.5 x 10^{-5} g L^{-1} concentration of 2-phenoxyethanol, then weighed using a Scout Pro balance (±0.1 g), and their total length measured; only length was recorded for other species caught.

Each site (individual channel or pool) was described by a range of habitat variables split into three categories including *abiotic stress factors*: pool permanence, depth, dissolved oxygen (mg/L ± 0.01, DO), conductivity (± 0.01 µS cm), pH (± 0.01) and temperature (± 0.1 ºC, T); *biotic factors*: number of banded kokopu present; *habitat heterogeneity factors*: overhead cover (OHC), submerged woody debris (SWD), dominant substrate type, overhanging vegetation (OHV), emergent tree roots (ETR) and habitat type. Pools were defined as permanent if they contained water during the dry sampling, and temporary if they had accumulated water since the dry sampling. Hence any fish caught in temporary pools were assumed to have survived a period of drought prior to the dry sampling. Pool volume (m^3) was calculated as pool area x average pool depth (m^2). Dissolved oxygen and T were measured using a YSI 550a meter, and conductivity and pH were measured using a YSI 63 meter at the pool bed. The YSI 63 was calibrated in the laboratory prior to each field trip, and the YSI 550a was calibrated after measuring each transect. Overhead cover was measured using a densiometer held at chest height over the centre of each site. Submerged woody debris was measured as the number of submerged wood pieces >30 cm length, and 2.5 cm width, as determined by sight, and OHV was measured as the presence/absence of plants overhanging a pool by >30 cm.

Dominant benthic substrate type was classified as either fine (grains <1 mm diameter) or coarse (grains >1 mm) depending on which type covered the greatest proportion of the pool bed. Emergent tree roots were measured as the percentage of the pools' circumference with visible roots extending into the water, where roots could range from those of large podocarps to small plants. Habitat type was classified as either a channel, or a tree-fall pool,

with nondescript depressions/pools described as 'other'. I used Adams and Norton's (1991) definition of tree fall pools. These authors described tree-fall pools as pits with adjacent mounds of earth resulting from the uplifting of soil from the tree fall event, a recognisable pattern for tree-falls aged <100 yrs in Saltwater Forest. Because OHC, SWD, OHD and ETR were assumed to be relatively constant over the dry/wet period, they were only measured once when the habitat was first encountered, and I used the minimum value of DO, pH, depth and T recorded between the two samples in subsequent analyses.

Data Analysis

Banded kokopu was the only species other than mudfish to be caught frequently. They were rarely found in pools containing mudfish, and never in temporary pools. Consequently, I focused my analysis on how habitat variables differed between pools with mudfish and pools with kokopu. Firstly, I reduced the number of habitat variables within each category (abiotic stress factors and habitat heterogeneity factors) to those that best explained mudfish distribution. I then contrasted how mudfish and kokopu presence differed in response to each variable in this refined list. Finally, I used the results of this analysis to develop and compare the performance of a set of candidate models designed to test my hypotheses about the relative importance of physiological stress and habitat heterogeneity factors.

To refine my list of habitat variables, I first built logistic regression models predicting mudfish presence/absence that contained all the variables within each category (excluding interaction terms). I then sequentially removed terms in order of their significance until the models with the lowest AIC_c (Akaike Information Criterion corrected for small sample size (Burnham & Anderson 2002)) were reached. This limited my subsequent analyses to: the presence of kokopu (biotic factors), pool permanence, depth, DO, pH (abiotic stress factors) and ETR and substrate type (habitat heterogeneity factors). I then compared how mudfish and

kokopu presence differed in response to these factors by constructing separate logistic regressions for each variable.

Using the results of this analysis, I developed a set of candidate models predicting mudfish distribution that combined the most important variables (kokopu presence, DO, pH, T, ETR and substrate type) in ways that tested my hypotheses. The performance of these candidate models was later compared using AIC_c and Akaike weights (w_i) (Burnham & Anderson 2002). Candidate models were of two types. 'Trade-off' models consisted of variables assumed to directly correlate with physiological stress (e.g. pool permanence, DO, pH and depth) and hence were used to examine a potential abiotic-biotic stress tolerance trade-off between mudfish and kokopu. Because kokopu were completely absent from temporary pools where mudfish were frequently found, all trade-off models included an interaction between pond permanence and DO, pH, and depth. The rationale for this was that, in temporary pools, the absence of kokopu would allow mudfish to exploit the less stressful range of its distribution (higher DO, pH and depth). In permanent pools however, kokopu presence is likely, and hence mudfish would likely be limited to stressfully low levels of oxygen and pH that kokopu cannot tolerate. Consequently, statistical interactions between pool permanence and pool chemistry would provide strong evidence for an abiotic-biotic tolerance trade-off between mudfish and kokopu.

Two trade-off models were developed. One model only included interactions between pool permanence and DO, pH, and depth, and their direct effects. A second model included these variables in addition to a kokopu presence/absence term. The rationale for this model was that if the interactions between the abiotic stress terms explained the mudfish-kokopu allopatric distribution sufficiently, then the addition of the kokopu presence/absence terms would explain very little additional deviance in mudfish distribution thus further testing the presence of an abiotic-biotic stress tolerance trade-off.

Trade-off models were compared to three 'other' models consisting of variables that were assumed to not affect physiological stress, or that simply indicated an allopatric distribution between fish that was not necessarily due to an abiotic-biotic tolerance trade-off. These models included combinations of the terms: kokopu presence/absence, ETR and substrate. Support for a model including only a kokopu presence/absence term would indicate that an allopatric distribution between kokopu and mudfish existed, but the distribution driver would be unknown. A model including an interaction between kokopu presence/absence and ETR plus substrate would indicate that an allopatric distribution was driven by habitat heterogeneity features (e.g. physical refugia for mudfish from kokopu within a habitat). Finally, a model including only ETR and substrate would indicate that there was no allopatric distribution, but that habitat heterogeneity features were an important driver of mudfish distribution. Analysis of each effect within a candidate model was undertaken using as it was entered last in the model due to the likelihood of shared deviance explained between variables.

Results

Mudfish distribution modeling

Brown mudfish and banded kokopu distributions were almost completely allopatric (Figure 1). This distributional asymmetry was centred on differences in fish species occurrence in temporary and permanent pools (Figure 2). Mudfish had a significantly higher occurrence in temporary pools (logistic regression: $D^2 = 0.17$, $\chi^2 = 16.11$, $P < 0.001$), being found in 88.5 percent of temporary pools, compared to 43.6 percent of permanent pools (Figure 2). Meanwhile kokopu were only ever found in permanent pools, and if present, mudfish presence was significantly less likely (logistic regression: $D^2 = 0.35$, $\chi^2 = 17.40$, $P < 0.001$) (Figure 2). In fact, only two permanent pools contained both species suggesting there

were mechanisms causing allopatry between mudfish and kokopu in permanent pools. The minimum length of mudfish was also significantly higher in pools with kokopu (mean: 114 ± 9 mm TL), compared to pools without (mean: 56 ± 3 mm TL, one way ANOVA: $R^2 = 0.31$, $F_{1,38} = 17.32$, $P < 0.01$).

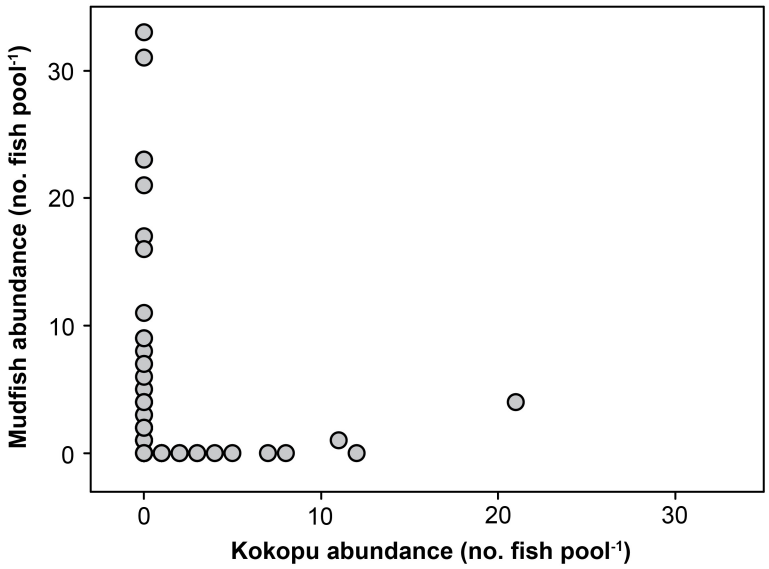


Figure 1: Banded kokopu and brown mudfish abundance from 65 forest pools in Saltwater Forest of South Westland, New Zealand.

Mudfish and kokopu allopatry in permanent pools appeared to be driven by water quality, with low oxygen and pH distinguishing pools with mudfish compared to pools with kokopu (Figure 3a, b). Within these permanent pools mudfish presence was significantly negatively associated with minimum pool oxygen (logistic regression: $D^2 = 0.17$, $\chi^2 = 8.99$, $P < 0.01$), and pH (logistic regression: $D^2 = 0.18$, $\chi^2 = 9.83$, $P < 0.01$) (Figure 3a, b), and significantly positively associated with the presence of fine sediment (logistic regression: $D^2 = 0.08$, $\chi^2 = 4.45$, $P = 0.035$) and ETR (logistic regression: $D^2 = 0.17$, $\chi^2 = 9.24$, $P < 0.01$). In contrast, kokopu presence in permanent pools was significantly positively associated with minimum pool oxygen (logistic regression: $D^2 = 0.16$, $\chi^2 = 8.55$, $P < 0.01$), and pH (logistic

regression: D^2 = 0.25, χ^2 = 12.67, P < 0.001) (Figure 3a, b) and significantly negatively associated with the presence of fine sediment (logistic regression: D^2 = 0.11, χ^2 = 5.62, P = 0.028), but was not related to ETR (logistic regression: D^2 = 0.038, χ^2 = 1.96, P = 0.162). Several other species were also present in some permanent pools, including: inanga (*Galaxias maculatus*) (four pools, DO: 1.74 +/- 0.70 mg/O_2/l, pH: 4.69 +/- 0.23), redfin bully (*Gobiomorphus huttoni*) (one pool, DO: 2.75 mg/O_2/l, pH: 4.73), and long fin eel (*Anguilla dieffenbachii*) (one pool, DO: 2.65 mg/O_2/l, pH: 4.21), however, they always co-occurred with kokopu, and never with mudfish.

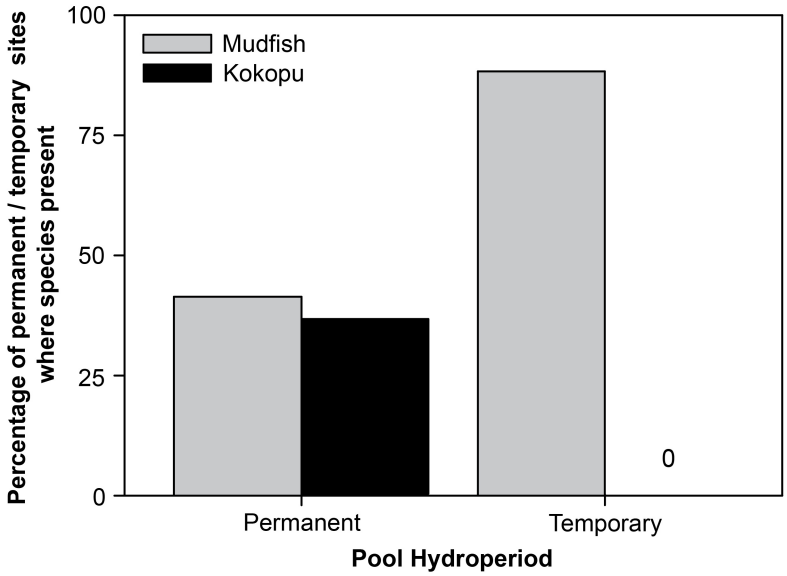


Figure 2: Percentage of permanent (n = 39) and temporary (n = 26) pools that contained brown mudfish (grey bars) or banded kokopu (black bars). Brown mudfish were present in 41.5 and 88 percent of permanent and temporary pools respectively. Banded kokopu were present in 36.6 percent of permanent pools but were completely absent from temporary pools (indicated by a zero).

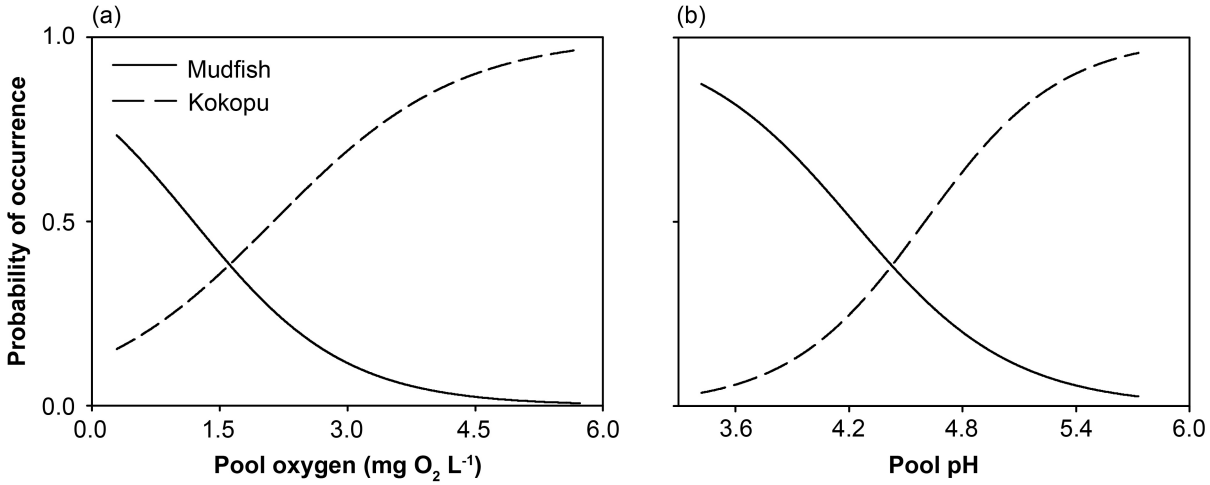


Figure 3: Predicted probability of occurrence of brown mudfish (continuous) and banded kokopu (dashed) in permanent pools as a function of minimum pool **(a)** dissolved oxygen and **(b)** pH. Probability of occurrence was calculated using separate logistic regression models of fish presence/absence based on either dissolved oxygen or pH measurements in forest pools.

The two models explaining mudfish distribution with the lowest AIC_c both included the abiotic stress terms involving an interaction between pool permanence and DO, pH and depth (Table 1). The akaike weights for the top two models totalled 0.97 suggesting there was a 97 percent chance that the best approximating model was contained within this pair, and there was only a three percent chance that the best model excluded the abiotic stress terms (Table 1). Kokopu presence explained 23 percent of the deviance in mudfish distribution when considered as a single variable (Table 1), indicating a strong allopatry between mudfish and kokopu. However, only four percent of extra deviance was explained by adding the kokopu presence/absence term with the abiotic stress variables in the top model (Table 1). Therefore, 83 percent of the deviance explained by kokopu presence can also be explained with the abiotic stress terms. The model including only abiotic stress variables also explained more total deviance than the model with kokopu presence alone (53 and 20 percent, respectively) and had a much larger akaike weight (0.40 and 0.001 respectively). This indicates that pool permanence, DO, pH and depth adequately explained the allopatric

distribution between mudfish and kokopu, and that knowledge of kokopu presence is not essential to determine likelihood of mudfish presence if these water quality parameters are known.

Table 1: Model selection results for the hypotheses evaluating abiotic and biotic controls on brown mudfish distribution. Pool permanence is a factor defining whether a pool is permanent or temporary, DO, pH and depth is a pools' minimum dissolved oxygen (mg O_2 L^{-1}), pH and depth respectively, banded kokopu presence is a factor defining whether kokopu were present or absent in a pool, emergent tree roots is the percentage of pool circumference with extruding plant roots, and substrate type is factor defining whether the pool had course or fine substrate. An asterisk indicates an interaction between the previous factor and all subsequent variables in brackets. D^2 is the full model's coefficient of determination, AIC_c is Akaike's information criterion corrected for small sample sizes and w_i is the model's Akaike weight.

Model	D^2	AIC_c	w_i
Pool permanence*(DO + pH + depth) + banded kokopu presence	0.57	58.46	0.56
Pool permanence*(DO + pH +depth)	0.53	59.10	0.40
Banded kokopu presence*(emergent tree roots + substrate type)	0.41	64.30	0.03
Banded kokopu presence	0.23	71.08	<0.01
Emergent tree roots + substrate type	0.19	76.68	<0.01

For the model containing only the effects of pool permanence and DO, pH and depth variables (Table 2) the direction of effects was consistent with the allopatric pattern of mudfish and kokopu I observed (Figure 2, 3a, b). DO and pH in temporary pools both had significant positive effects on the likelihood of capturing mudfish (Table 2, Figure 4a, b), where kokopu were never found (Figure 2). In contrast, the relationship between mudfish presence and DO and pH was negative in permanent pools (Table 2, Figure 4a, b), where kokopu were more likely found (Figure 2), as indicated by the significant interactions between pool permanence and DO and pH (Table 2). This suggests the effects of DO and pH

on mudfish presence were dependent on how they affected kokopu presence and provides support for an abiotic-biotic trade-off driving the allopatric distribution of mudfish and kokopu. Interestingly, the direct effect of permanent pools was negative when this was considered as a single variable (Figure 2), but was positive when considered in light of the negative effects of DO and pH in permanent pools (Table 2). This indicates that high DO and pH explain why mudfish were absent from a substantial number of permanent pools. Thus mudfish presence is highly likely in a permanent pool as long as the water has low enough DO or pH to prevent kokopu establishment.

Table 2: Coefficient and deviance table for the second model shown in Table 1, which includes the interaction between pool permanence, and pool DO, pH and depth, and their direct effects. The model coefficients (and their standard errors, S.E.), coefficients of determination (D^2) and chi-square values, from which significance (*P*) was determined, were calculated as terms entered last in the model.

Variable	Coefficient	S.E.	D^2	χ^2	*P*
Permanent pools	77.76	46.73	0.24	21.6	<0.001
pH (in permanent pools)	-19.61	11.48	0.12	10.8	<0.010
pH (in temporary pools)	15.14	11.34	0.09	8.1	<0.010
DO (in permanent pools)	-1.91	0.92	0.07	6.3	0.010
DO (in temporary pools)	0.65	0.70	0.05	4.5	0.019
Depth (in permanent pools)	39.74	21.75	0.05	4.5	0.030
Depth (in temporary pools)	-33.85	21.55	0.04	3.6	0.055

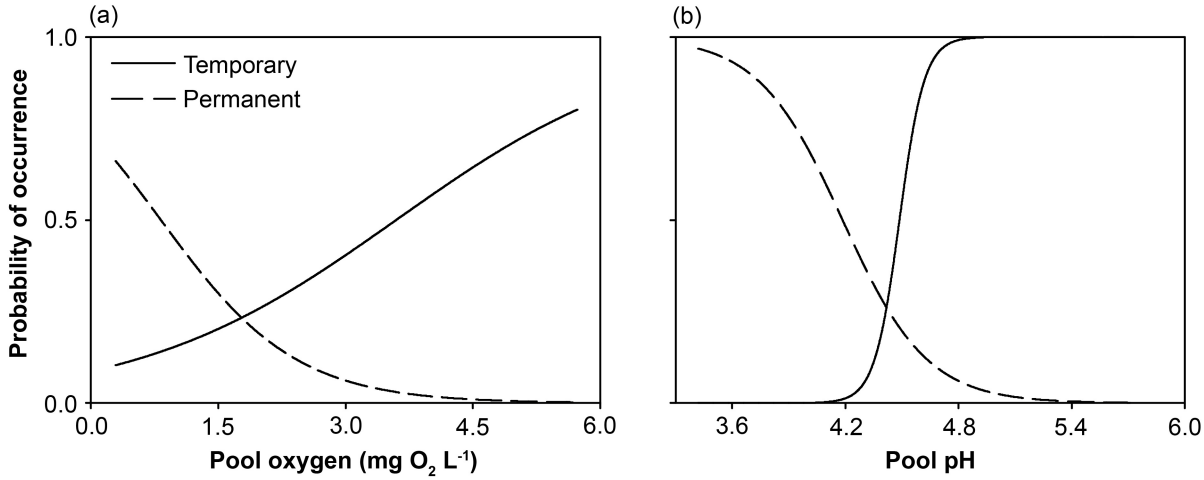


Figure 4: The logistic regression estimated probability of brown mudfish occurrence as a function of the interaction between pool permanence and **(a)** pool dissolved oxygen, and **(b)** pool pH in model 2 from table 2. Pool depth was held constant at the mean depth of all 65 pools for all regressions, and dissolved oxygen and pH was held at their mean values when estimating the effect of pH or dissolved oxygen respectively.

Discussion

The degree to which a species is tolerant to multiple environmental extremes may be an important mechanism controlling species responses to global environmental changes. I found that multiple environmental extremes were important determinants of the distribution of a threatened extremophile freshwater fish, the brown mudfish. Permanent pools, high pH, and high oxygen all had counter-intuitive negative effects on brown mudfish presence that could only be explained by their positive effects on the mudfish's most common competitor/predator, banded kokopu. Thus, environmental extremes indirectly determined mudfish distribution by their direct effects on kokopu presence. Each effect was statistically independent, suggesting each extreme offered complementary refuge to mudfish from kokopu and thus caused a habitat portfolio effect on the mudfishes realised niche. Thus, the negative effects of species interactions in benign conditions explained almost all deviance in extremophile distribution.

Drought constitutes one of the greatest stresses to freshwater fish due to its negative effects on multiple physiological systems, including oxygen delivery, water and ionic balance and nitrogenous waste excretion (Chew *et al.* 2004; LeBlanc *et al.* 2010; Urbina & Glover 2013). Consequently, drought endurance requires specialised investment in physiological adaptations that are important determinants of species assembly sorting (Chase 2007), but which are traded-off with vulnerability to competition and predation in permanent water bodies (Welborn, Skelly & Werner 1996). I therefore predicted that temporary pools would provide the greatest level of refuge against kokopu for the brown mudfish. This prediction was supported by a significant 45 percent increase in the likelihood of mudfish capture in temporary pools. Only twelve percent of temporary pools did not contain mudfish, in contrast to the 56 percent of permanent pools. Meanwhile, temporary pools appeared to eliminate banded kokopu, which were completely absent from habitats that dried. This effect was strong enough to prevent kokopu occurrence in temporary pools containing mudfish that were only metres away from kokopu source pools. Thus mudfish and kokopu allopatry was driven by abiotic stress at a very fine scale. This contrasts with recent biogeographic theory, which suggests species interactions should be a dominant controlling factor at local scales, and abiotic factors should be more important at macro-ecological scales (Pearson & Dawson 2003). Instead, my observations suggest species interactions and abiotic factors are both important at very fine scales where they interact with each other. This is more in line with the species-sorting paradigm in meta-community theory, which focuses on trade-offs between species that adapt species for local patches that are heterogeneous for different abiotic conditions (Leibold et al. 2004). Thus membership of a patch or pool is determined by the outcome of species interactions, which are dependent on certain abiotic conditions (Leibold et al. 2004), in my case, drought.

The significant interactions between pool permanence and DO and pH are evidence

that such species-sorting mechanisms may involve multiple physiological stressors. I showed that the direction of the effects of DO and pH on mudfish presence were dependent on where kokopu were found (permanent pools with high DO and pH). Thus mudfish showed positive associations with DO and pH in temporary pools where kokopu were absent, but negative associations in permanent pools where kokopu were present. In fact, the negative effect permanent pools had on mudfish presence when it was considered as a single variable was reversed after the interaction between pool permanence and DO and pH was added to the model. This could happen if high DO and pH were explaining why mudfish were absent from most of the permanent pools. These pools had relatively benign levels of DO and pH making it more likely that the presence of kokopu in these pools were limiting mudfish rather than high DO and pH directly. That the majority of the deviance explained by kokopu presence/absence was shared with the pool permanence and DO and pH interaction terms also supports this conclusion. Mudfish were significantly larger in pools containing both species suggesting kokopu predation of mudfish juveniles may be a mechanism preventing mudfish establishment in benign pools. This indicates that mudfish may have a much larger fundamental niche than is indicated by their distribution (Figure 5a), but due to the presence of kokopu in benign conditions they have a severely restricted realised niche that is limited to extreme conditions (Figure 5b). However, three key abiotic extremes (drought, hypoxia and acidity) each explained significant independent amounts of deviance in mudfish distribution, suggesting their effects were complementary, and hence increased the size of the mudfish realised niche beyond that of a single stress (Figure 5b – d). This created a habitat portfolio effect of abiotic refugia (Figure 5b - d).

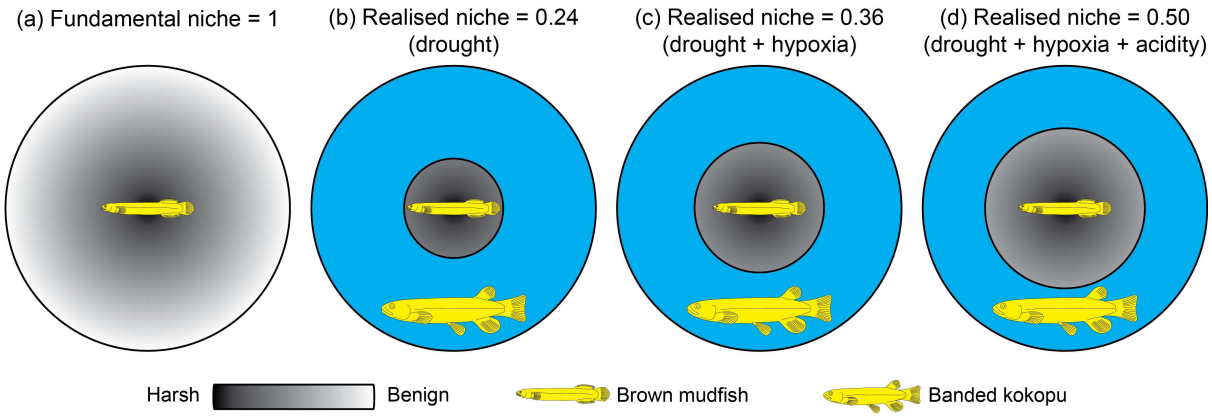


Figure 5: The effects of abiotic and biotic constraints on the distribution of an extremophile, the brown mudfish. The numbers represent the realised proportion of the fundamental niche occupied by mudfish, which is dependant on the presence of kokopu and the number of abiotic stressors controlling their relative distribution. Realised niche is the sum of the proportion of deviance in mudfish distribution explained by each stressor in brackets calculated from Table 2. Being tolerant of extreme abiotic stress, mudfish are expected to have a large **(a)** fundamental niche and be physically capable of inhabiting both harsh and benign ends of abiotic gradients. Because banded kokopu are present in benign habitats (blue) **(b)**, we instead observe that mudfish are restricted to a severely limited niche associated with harsh abiotic conditions, particularly temporary pools, thus generating a large fundamental-realised niche ratio. However, this realised niche additionally consists of both **(c)** hypoxia and **(d)** acidity in permanent pools, which offer complementary refuge against kokopu predation thus enlarging the realised niche beyond a single stressor. Fish illustrations were re-drawn from (McDowall 2006).

Comparison of my data with the pH distributions for 15 other New Zealand freshwater fish species reveals that large fundamental niches are a consistent feature of species tolerating extreme stress (Figure 6). I found mudfish at a minimum pH of 3.36, which is the lowest pH published for a New Zealand freshwater fish (Collier et al. 1990; Greig et al. 2010). However, the maximum pH they have been previously found in matches that of other fish (~7.5) (Francis 2000), which is largely invariant between species (Collier et al. 1990; Greig et al. 2010). Thus the maximum pH range for each species declines in direct proportion

to the minimum pH they are found in (Figure 6). Although species distributions from field observations are not a true measure of fundamental niche (Guisan & Zimmermann 2000; Pearson & Dawson 2003; Guisan & Thuiller 2005), the pH ranges discussed here may be indicative of fundamental pH niche due to the large number of sites from which they were drawn from, which included over 3100 stream reaches and wetland sites throughout New Zealand (Greig et al. 2010). Hence, this strongly suggests that species fundamental niches are positively correlated with their investment in stress tolerance.

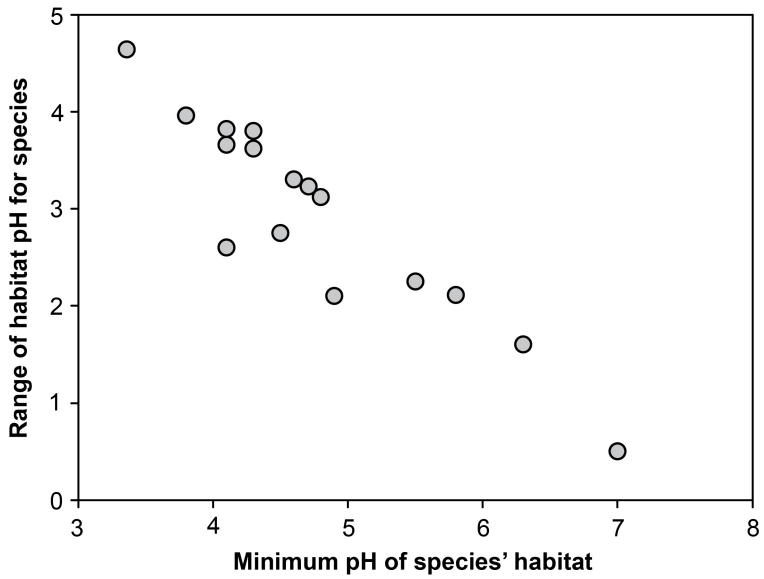


Figure 6: The significant negative relationship between the minimum habitat pH of a species and the maximum pH range they are found in for 16 New Zealand freshwater fish species (R^2 = 0.87, $F_{1,15}$ = 97.71, P < 0.001). Data sources include Greig et al. (2010) and O'Brien and Dunn (2007) and references therein, and this study, which used qualitative and quantitative electric fishing, night spotlighting, traps and nets to survey fish occurrence in a over 3100 streams and wetlands throughout New Zealand.

This negative correlation between a species' minimum and maximum habitat pH may have a physiologically driven explanation. Lowering pH, particularly below 4, increasingly disrupts sodium homeostasis (Glover, Donovan & Hill 2012), often leading to death by lack

of internal sodium (Wood 1989). Tolerance of low pH thus requires specialised adaptations that reduce sodium efflux or increase sodium influx to the organism (Wood 1989). These traits should not reduce maximum pH tolerance, at least not until pH 9-10 where both ammonia excretion and sodium uptake become impaired (Wilkie, Simmons & Wood 1996). Thus, while minimum pH tolerance is mediated by physiological mechanisms, maximum pH tolerance up to neutrality should remain invariant, thereby generating the fundamental niche pattern observed here. Such patterns should be replicated for other stressors such as hypoxia and drought, which have clearly defined stressful and benign ends.

Despite the large potential niche that extreme physiological tolerance can provide, many species are frequently absent from the benign conditions of their niche (Holway, Suarez & Case 2002; Alcaraz, Bisazza & García-Berthou 2008; Krassoi *et al.* 2008). While dispersal and biogeographical constraints explain some absences (Guisan & Thuiller 2005), they are often due to antagonistic interactions between species (Davis et al. 1998; Vetaas 2002). Species richness is often higher in benign habitats, thus providing additional biotic stress from competition and predation as abiotic conditions become more benign (Dobzhansky 1950; Pianka 1966; Southwood 1977; Greenslade 1983). The positive relationship between stress tolerance and fundamental niche (Figure 6) indicates that there are a greater number of species potentially present in benign environments because more species can survive these conditions. Consequently, the strength of biotic, and random dispersal forces determining community membership is likely to increase as habitats become more benign (Chase 2007).

Species that are limited to stressful realised niches are frequently the most threatened by extinction because alternative habitats are limited (Giam et al. 2012). I have found that an extremely tolerant species may be able to use multiple stress tolerances as a way to increase their realised niche, which could enhance their security in the face of environmental change. My study indicates brown mudfish, an extremophile species endemic to the peat-swamp-

forests of New Zealand, are restricted to extreme environments due to the negative impact of biotic interactions in benign environments. Drought, hypoxia and acidity all contributed independently to the realised niche of the brown mudfish, which suggests they have a large fundamental to realised niche ratio. Habitat loss in their peat swamp forests typically consists of deforestation followed by wetland drainage (McDowall 2006), which my data suggests represents an increasing scale of realised niche loss for these extremophile fish. Such complementarity amongst niche components may, therefore, create a habitat portfolio effect, whereby the absence of one stressor could be replaced by another. Understanding extremophile response to future environmental change should focus on how such crucial aspects of their realised niche are altered.

Chapter Three

Deviations from the metabolic theory of ecology drive local distribution and abundance in forest-pond-dwelling extremophile fish

Abstract

The Metabolic Theory of Ecology (MTE) predicts negative three quarter power scaling of maximum population density with species mass because of the positive three quarter power scaling of metabolism with mass. However, there is large inter-specific, mass-independent, variation in metabolic rates which MTE does not account for. This variation may be important at local levels, where factors specific to locations or species may complicate MTE predictions. Habitat templet (HTT) and maximum power (MPT) theories may solve this problem by explaining how metabolic rates vary between species as a function of their environment. I tested the predictions of HTT and MPT theories that fast versus slow metabolism in species results from an abiotic-biotic tolerance trade-off. I studied brown mudfish (*Neochanna apoda*) and banded kokopu (*Galaxias fasciatus*), which are forest-pond-dwelling fish, distributed along an abiotic stress gradient involving extreme drought, hypoxia and acidity. I also evaluated whether species mass-specific metabolic differences could account for mass-specific population density variation for the relationship between mass and population density for mudfish and kokopu. As predicted, mudfish had significantly lower maximum (MMR) and resting (RMR) mass-specific metabolic rates compared to kokopu at all sizes measured. This explains the mudfish's strong tolerance to abiotic stress, but sensitivity to antagonistic interactions with kokopu, and thus the allopatric distribution of the two species in pools varying in environmental harshness. The low mudfish mass-specific RMR also accounted for their significantly higher mass-specific population densities compared to kokopu. Thus mudfish and kokopu population densities were equivalent once

their metabolic adaptations to local environmental stressors were accounted for. Overall I show how local ecological contingency can be explained and incorporated to enable the macro-ecological scale predictions of MTE to be locally relevant.

Introduction

The metabolic theory of ecology (MTE) is a macro-ecological theory that has been the focus of intense interest and research in the past decade (West, Brown & Enquist 1997; West, Brown & Enquist 1999; Gillooly *et al.* 2001; Brown *et al.* 2004). Metabolic theory predicts one quarter power scaling of ecological phenomena with individual or species mass because of the fundamental three quarter power scaling of mass with resting metabolic rates (RMR) (Brown et al. 2004). For example, because RMR (or consumption rates) increases with an individual's mass with a slope of 0.75, maximum population density should decline with the average mass of individuals in a population with a slope of –0.75 (Damuth 1981; Brown *et al.* 2004). This reasoning invokes an additional fundamental concept, that maximum population carrying capacity (C), all else being equal, should equal energy availability (E) divided by the per-capita consumption rate (P_c) (i.e. $C = E / P_c$) (Damuth 1981; Carbone & Pettorelli 2009). Consequently, as mass increases, E is divided by an increasingly larger number (i.e. $P_c = \text{mass}^{0.75}$), and therefore, C must decline (i.e. $C = \text{mass}^{-0.75}$) (Damuth 1981; Brown *et al.* 2004).

While this metabolic principle has had some support at large ecological scales (Damuth 1981; Nee et al. 1991), there is still large residual variation in its predictions for specific species and locations (Blackburn & Gaston 1999). Moreover, as mass range declines to that which is more likely at local scales, this residual variation in density that is unexplained by mass increases relative to that which is explained by mass (Isaac, Storch & Carbone 2013), and the slope of the size-density relationship (SDR) can fluctuate greatly

(Isaac, Storch & Carbone 2011). Consequently, the applicability of mass as a universal predictor of density may be limited at small scales, where location and species-specific knowledge may be more predictive. Understanding how metabolism varies between species independently of mass as a result of environmental gradients may help explain residual variation in density that is unexplained by mass to allow MTE to be more relevant at local scales.

Habitat Templet (HTT), and Maximum Power (MPT) theories provide frameworks for predicting this variation because together they define the context within which a fast or slow metabolic rate (fast-slow metabolism) may evolve in a species (Lotka 1922; Southwood 1977; Greenslade 1983; Southwood 1988). MPT predicts that biological systems will organise to maximise energy flux within environmental constraints (Lotka 1922; Odum & Pinkerton 1955), a concept grounded in successional theory (Odum 1969). Thus MPT provides an energetic definition of fitness by linking consumption rates with life-history traits such as growth rates and reproductive output (Brown, Marquet & Taper 1993). While life-history parameters and inter-specific dominance are often positively correlated with metabolic rates (DeLong 2008; Biro & Stamps 2010), the relationships are heavily context-dependant implying there is a fast versus slow metabolic trade-off determined by the environment (Burton et al. 2011). The environmental context for such a trade-off is provided by HTT theory, which predicts that life history traits (e.g., growth and reproductive rates) will correlate positively with biotic stress (e.g., competition/predation) and negatively with environmental stress (Southwood 1977; Greenslade 1983; Southwood 1988). Thus an abiotic-biotic tolerance trade-off is the primary force selecting for fast versus slow life-histories under HTT (Figure 1a).

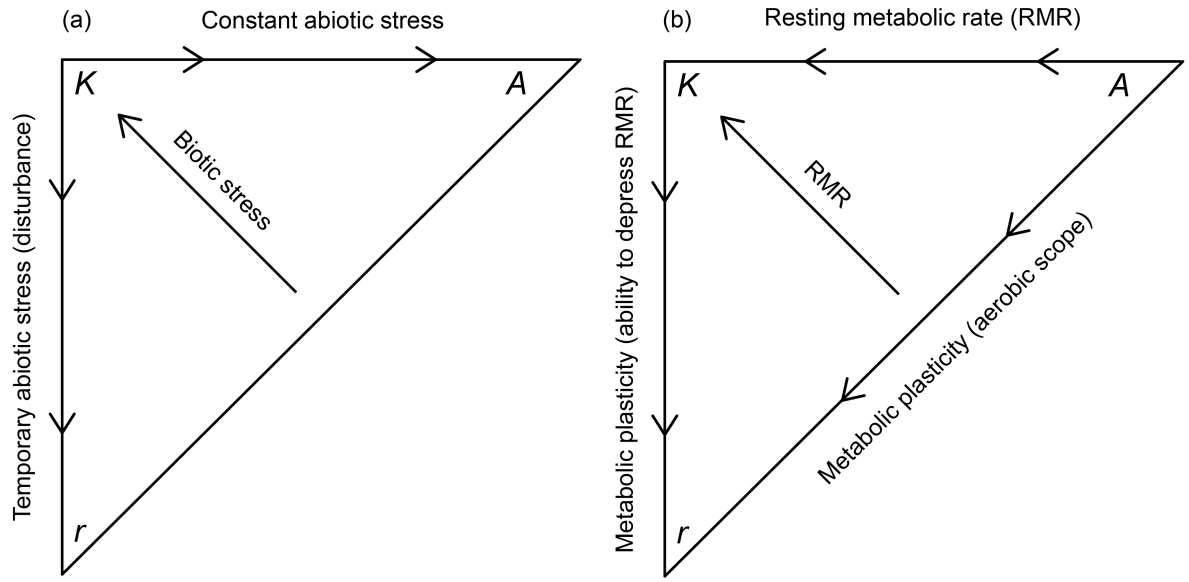


Figure 1: a) The Southwood-Greenslade habitat templet, adapted from Southwood (1988) to highlight the distinction between, temporary and consistent abiotic stress, and biotic stress, which increases as temporary and constant abiotic stress decrease. Individual and population growth rates and reproductive output decreases from *K*- to *A*-selected species (i.e. fast versus slow life-histories) as abiotic conditions become constantly more stressful (i.e. mesic to arid), and biotic stress (e.g. competition) declines. Temporally fast life-histories evolve (i.e. those traditionally called *r*-selected) where conditions fluctuate between environmentally stressful and benign conditions so as to capitalise on short favourable growth periods. Because growth and reproduction requires energy, these life-history strategies may translate into the metabolic traits in **(b)**, with low mass-specific RMR (resting metabolic rates) for *A*-selected species living in constant energy stress, and high RMR for *K*-selected species living in competition/predation-intense habitats with high species richness. High metabolic plasticity (i.e. aerobic scope or metabolic depression) may occur in *r*-selected species allowing them to capitalise on benign periods for rapid growth (high aerobic scope), but tolerate periods of abiotic stress by temporally depressing RMR. *K*-selected species may also have a high aerobic scope to enhance foraging and predation capacity, but are predicted to lack metabolic depression ability because of the lack of temporary stress.

Habitat templet theory defines environmental stress primarily as low habitat productivity, however, this may also include any abiotic factor that reduces an organism's

capacity to acquire or use energy to maintain homeostasis regardless of the availability of habitat energy (Southwood 1988). For instance, hypoxia limits redox potential for oxidative phosphorylation leading to inefficient anerobic substrate consumption, while the increased thermodynamic stability of enzymes at low temperatures reduces the rate at which enzymes can consume ATP (Hochachka 1986; Hochachka 1988). Environmental stress can also be permanent or temporary, for instance, drought temporarily induces aquatic hypoxia, desiccation and starvation (Bond, Lake & Arthington 2008; Urbina & Glover 2013). Because these are all ultimately forms of energy stress, a low RMR is likely to increase survival of organisms experiencing them (Figure 1b) (Hochachka 1986; Hochachka 1988). However, whether low metabolism is fixed or flexible may depend on the temporal nature of abiotic stressors. For instance, species subjected to temporary stress punctuated by benign periods may be capable of increasing their metabolism to capitalise on favourable growth periods (Figure 1b) (Welborn, Skelly & Werner 1996). Because these predictions are based on differences in local conditions, they may be useful frameworks for adapting MTE to specific localities (McGill et al. 2006). In particular, this framework predicts higher mass-specific population densities for species tolerant to abiotic stress because of a lower mass-specific consumption rate, and thus a higher intercept for their size-density relationship (SDR) under MTE.

I applied HTT and MPT theories to two freshwater fish species, whose distribution is driven by an abiotic-biotic tolerance trade-off. The brown mudfish (*Neochanna apoda*) and banded kokopu (*Galaxias fasciatus*) are forest-pond-dwelling fish distributed along an abiotic stress gradient involving extreme drought, hypoxia and acidity (Chapter 2). Brown mudfish are restricted to the harsh end of this gradient because of antagonistic biotic interactions with kokopu, to which they are highly sensitive (Chapter 2). I predicted that this abiotic-biotic tolerance trade-off was mediated by a fast-slow metabolic trade-off, with mudfish having

significantly lower resting and maximum metabolic scaling intercepts and slopes compared to the more powerful kokopu. I also evaluated whether variation in RMR scaling intercepts and slopes could explain inter-specific differences in mudfish and kokopu population size-density relationships (SDRs). I present evidence describing how species mass-specific metabolic rate adaptations to environmental conditions can explain local ecological contingency and thus allow the macro-ecological scale predictions of MTE to be locally relevant.

Methods

Metabolism

Animal collection and maintenance

Brown mudfish and banded kokopu were caught using Gee minnow traps (GMT) placed overnight in pools and streams located in the West Coast region, near Hokitika New Zealand. Fish were held in static 20 L plastic containers containing aerated freshwater, maintained at constant temperature (14 °C) and light conditions (12h : 12h). Fifty percent water changes were made daily and fish were fed *ad libitum* on commercial bloodworms (Aqua One®, Sydney, Australia), until three days before experimentation. All procedures were approved by the University of Canterbury Animal Ethics Committee.

Estimating resting and maximum metabolic rate, and aerobic scope

Resting metabolic rates (RMR) and maximum metabolic rates (MMR) were measured on each individual fish by measuring the rate of oxygen uptake using closed box respirometry before and after exhaustive exercise, respectively. Aerobic scope was then determined from the difference in RMR and MMR. Individual fish were acclimated to their respirometers (0.10 L, 0.25 L, 0.50 L or 1 L glass Schott bottles [Schott®, Elmsford, North America], depending on fish mass) for 12 h overnight with continuous water flow prior to measurement.

The respirometers were immersed in a water bath maintained at 14 °C at all times, and were sealed using rubber bungs after acclimation.

RMR was measured in 26 mudfish (0.4 – 15.9 g) and 29 kokopu (0.5 – 24.8 g) by comparing the change in oxygen concentration between water samples (0.7 ml) taken at 20 minute intervals from each respirometer. Samples were withdrawn with a syringe and injected into an MC100 microcell (Strathkelvin Instruments®, Glasgow, Scotland) containing an SI 130 oxygen electrode (Strathkelvin Instruments®, Glasgow, Scotland). The oxygen electrode was connected to an oxygen meter (SK Model 781, Strathkelvin Instruments®, Glasgow, Scotland), with output recorded on a computer via a Powerlab 4/SP (ADInstruments®, Richmond-Windsor, Australia). The electrode was calibrated daily before measurements using fully aerated water and a saturated sodium sulphite solution. Water from the water bath was pumped through the microcell water jacket so that water samples were maintained at 14 °C during measurement. The rate of oxygen consumption was calculated as:

$$MO_2 = \frac{\Delta O_{2i} \cdot \alpha O_2 \cdot \mu O_2 \cdot V_i}{\Delta T}$$

where ΔO_{2i} is the change in oxygen partial pressure (torr) in fish *i*'s respirometer between samples, αO_2 is a constant reflecting the solubility of O_2 in freshwater at 14 °C (2.0518 μmol L^{-1} $torr^{-1}$), μO_2 is the molecular mass of oxygen (31.99 μ), V_i is the volume (L) of fish *i*'s respirometer and ΔT is the time interval between samples.

A subset of 24 mudfish and 19 kokopu were then measured for their MMR immediately following determination of their RMR. MMR was determined after individuals were exhaustively exercised using a forced swimming protocol similar to that of MacKenzie and colleagues (1996). Individual fish were transferred from their respirometers to a separate water bath maintained also at 14 °C and then manually chased for 15 - 20 minutes until exhaustion. Fish were considered to be exhausted when they were no longer capable of

escaping by burst swimming and could only make weak body movements. This exercise method was necessary because mudfish could not be forced to swim against an artificial current created in a swim tunnel. However, manual chasing has previously yielded comparable results to those generated by forced swimming (Killen et al. 2007). Immediately after exhaustion, fish were returned to their respirometers and MMR was measured using the same protocol described for RMR. However, for MMR, I used a 15 minute sample interval, and metabolism was repeatedly measured until RMR levels were reached. This estimates MMR based on the excess post-exercise oxygen consumption, which closely matches MMR. Fish were then weighed in grams (± 0.01) and returned to their aquariums. Aerobic scope was then calculated as MMR_i/RMR_i which represents the factorial increase of MMR over RMR for fish *i*.

Determining population sizes

Study site description

Fish abundance was determined in 39 mudfish and 25 kokopu pools in the Saltwater Forest, Westland National Park, South Island, New Zealand during the austral summer of 2011 - 2012. Saltwater Forest is a low altitude (20 - 100 m ASL) 9000 ha temperate peat-swamp-rainforest with high annual rainfall (3742 mm) (Rogers 1999). Poor soil drainage allows many small shallow pools to form on the forest floor, which may be permanently or intermittently flooded. Most pools are excavated by tree fall events, which uproot large amounts of soil, and generally do not exceed 0.3 m depth and 2.5 m^3 in volume.

Pools were located within four randomly positioned 100 - m long transects, which were stratified by altitude. Pool volumes were calculated by multiplying pool surface area (±0.01 m) by average pool depth (±0.01 m). Pool surface area was estimated using the formulas for an ellipse, square, circle or semi circle depending on pool shape or some

combination thereof for irregularly shaped pools. Surface areas and depths were measured for all pools on the same day to avoid bias caused by temporal variation in pool volume. Four mudfish and four kokopu pools were randomly selected for continuous temperature measurement during the sampling period, using one WT-HR stage/temperature logger (TruTrack, Christchurch, New Zealand) per pool. Temperature was logged in at least one pool in each transect, and water temperature was recorded hourly in each of these pools from 29 November 2011 to 23 March 2012. Fish populations within pools were sampled using un-baited 3.12 mm (1/8") mesh Gee minnow traps (420 mm L x 220 mm W) set for 12 h overnight at a constant density of 1 trap 2 m^3 of the pool surface area. Upon capture, all fish were anesthetised with a 0.5 x 10^{-5} g L^{-1} concentration of 2-phenoxyethanol, weighed using a Scout Pro scale (±0.1 g) (Ohaus®, Pine Brook, North America), and their total length measured (±1 mm).

Population size estimation

Population biomass was estimated by summation of the weights all individual fish caught in a pool on a single trapping night. Weights for individual fish were estimated using original length-wet mass regressions. Population biomass was divided by pool volume to estimate population biomass density (±0.1 g m^3). To investigate the assumption that my population biomass density estimates were unbiased towards either species, I conducted a mark-recapture survey of a subset of 33 mudfish pools and 16 kokopu pools. Pools were sampled using the same protocol as described above, but all fish caught on the first sample were uniquely marked using a combination of visual implant elastomer tags (Northwest Marine Technology, Inc, Shaw Island, North America) for fish <80 mm and passive inductive transponder tags (Oregon RFID, Portland, USA) for fish >80 mm. Sampling was repeated following a three to five day interval and the number of marked and unmarked fish

was counted. For each site, I compared the total density of fish caught on sample one (sample one density) with the total density of unique fish from samples one and two (total population density). A homogeneity of slopes test showed that there was no significant difference in the slope of the relationship between total population densities and the sample one densities for mudfish and kokopu (R^2 = 0.97, $F_{1,45}$ = 0.0004, P = 0.98); both slopes were approximately 0.95 ± 0.025 g m^3 (Appendix 1). Thus the densities estimated from a single trapping event equated to approximately 95% of the total population densities for both species and was unbiased.

Data analysis

Metabolic scaling

RMR and MMR values were treated as mg O_2 h^{-1}, thus all values were absolute rather than mass-specific unless otherwise stated. RMR, MMR and AS values were all $\log_{10}$-transformed for each fish and were regressed against the $\log_{10}$ of the fish mass (g). A homogeneity of slopes test was first used to test for species-specific differences in slopes using an interaction between species identity and the $\log_{10}$ of fish mass for all metabolic metrics. If interaction terms were not significant, I ran an ANCOVA with interaction terms removed.

Effects of metabolic rates on population densities

The RMR scaling relationships determined above for mudfish and kokopu were used to estimate the metabolic rate of each fish caught in each population based on their mass and species identity and was treated as mass-specific metabolic rate (mg O_2 g^{-1} h^{-1}). A one-way ANOVA showed that the average daily maximum temperature in mudfish pools (13.9 ± 0.4 °C) was not significantly different to that in kokopu pools (13.5 ± 0.5 °C, $F_{1,6}$ = 0.46, P =

0.52), and was close to the temperature used to derive the RMR scaling relationship (14 °C). Thus, ttemperature corrections were not applied to my population RMR estimates. The $\log_{10}$ of the average RMR of individuals in each population (log[μRMR]) was then calculated from these data. The $\log_{10}$ average mass of individuals in each population (log[μMASS]) was also calculated. Finally I calculated the $\log_{10}$ population biomass density for each pool sampled.

In testing predictions made by MTE it is important to include potentially correlated variables in the same model (Brown et al. 2004). I was interested in the relative variance in population biomass density explained by log(μRMR) compared to the variance explained the combination of species identity, log(μMASS) and their interaction. If interspecific variation in metabolism was responsible for interspecific variation in population biomass density, then log(μRMR) should explain the same variation in density as the combination of log(μMASS), species identity and their interaction. In this case, log(μRMR) would be the only variable necessary, and log(μMASS) and species identity would be removed in the process of model simplification. Thus I ran two model simplification analyses starting with two alternative full ANOVA models that depicted two cases. In Case One, where log(μRMR) was excluded, the starting full model included species identity and log(μMASS) direct effects and their interaction as predictors of log population biomass density. In the second model (Case Two) I included these effects in addition to the main effect of log(μRMR), and its interaction with species identity. Predictive terms were removed from each model starting with non-significant interaction terms, followed by the least significant main effects based on a type II sums of squares ANOVA. Terms were left out if their removal resulted in a lower AIC_c (Akaike's information criterion corrected for small sample size). Finally, I compared the strength of support for the two simplified models from Case One and Two using R^2, AIC_c, and Akaike weights (w).

Results

Metabolism

Resting metabolic rate

The slope of the relationship between RMR and mass was significantly greater for banded kokopu than for mudfish (Homogeneity of slopes test: $F_{1,50}$ = 4.53, P = 0.038) (Figure 2a). Thus for mudfish (BM), and banded kokopu (BK), the relationship between RMR and mass was best described by the equations:

$$RMR_{BM} = 0.11M^{0.62}$$

$$RMR_{BK} = 0.17M^{0.72}$$

where RMR is in mg O_2 h^{-1}, and M is fish mass in grams. The average mass of all fish measured for RMR was 6.7 g. At this weight, these equations predict kokopu will consume 1.9 times more oxygen (0.67 mg O_2 h^{-1}) than mudfish (0.36 mg O_2 h^{-1}) at rest.

Maximum metabolic rate

The slope of the relationship between MMR and mass was significantly greater for kokopu than mudfish (Homogeneity of slopes test: $F_{1,39}$ = 10.93, P < 0.01) (Figure 2b). Thus for BM and BK, the relationship between MMR and was best described by the equations:

$$MMR_{BM} = 0.16M^{0.77}$$

$$MMR_{BK} = 0.35M^{1.00}$$

where MMR is in mg O_2 h^{-1}, and M is fish mass in grams. Thus at 6.7 g, these equations predict kokopu will maximally consume 3.4 times more oxygen (2.35 mg O_2 h^{-1}) than mudfish (0.69 mg O_2 h^{-1}).

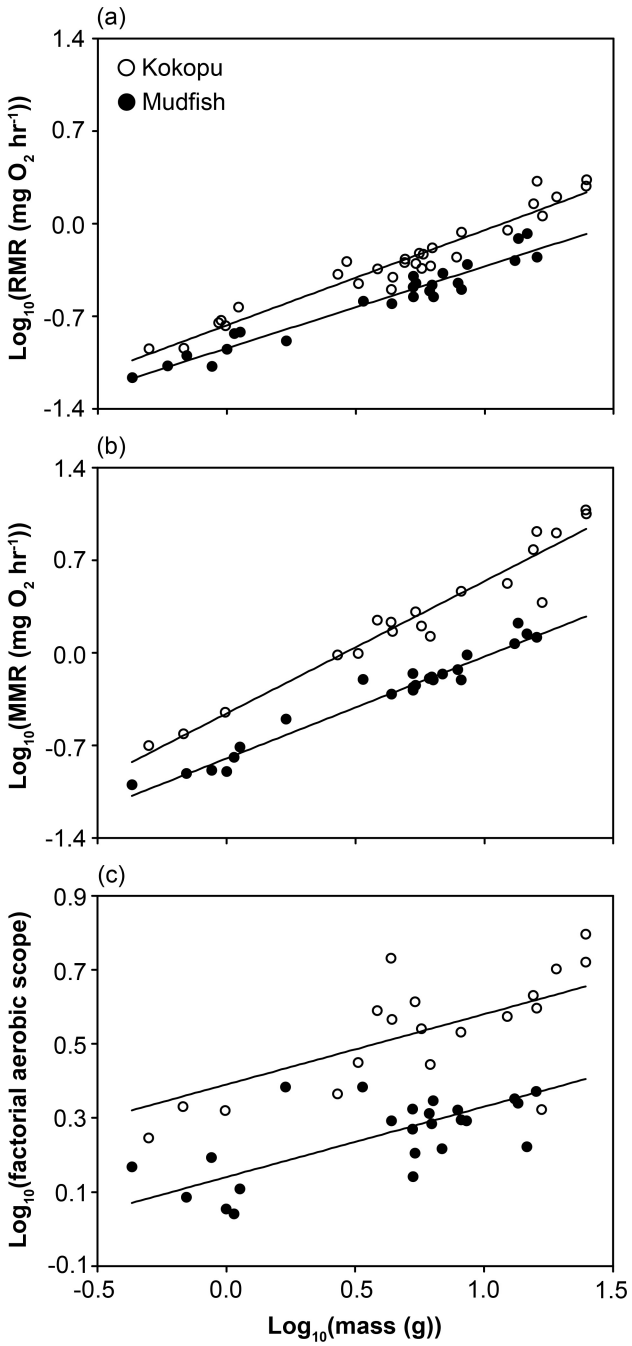


Figure 2: The effect of fish mass, on **(a)** resting metabolic rates (RMR), **(b)** maximum metabolic rates (MMR) and **(c)** factorial aerobic scope (i.e. MMR_i/RMR_i for fish i), for mudfish (closed circles) and kokopu (open circles). All data points are for individual fish. Slopes and intercepts were calculated from ANOVAs when species x mass interaction terms were significant and ANCOVAs when interactions were non-significant. The X axes are identical for all plots and y axes are identical for plot (a) and (b) and all are log_{10}-transformed.

Aerobic scope

There were no differences in the slopes of the relationship between AS and mass for BM or BK (Homogeneity of slopes test: $F_{1,39}$ = 1.50, P = 0.23) and AS was significantly lower for BM than BK for all sizes (ANCOVA species effect: $F_{1,40}$ = 69.43, P < 0.001) (Figure 2c). Thus for BM and BK, the relationship between AS and mass was best described by the equation

$$AS_{BM} = 1.38M^{0.19}$$

$$AS_{BK} = 2.45M^{0.19}$$

where y is AS (i.e. MMR/RMR), and M is fish mass in grams. Thus at 6.7 g, these equations predict that kokopu can more than triple its RMR (3.5x RMR) if needed, whereas mudfish can only double theirs (2.0 x RMR) if needed, which is a 1.75 x difference.

Effects of metabolism on population density

Mudfish had a lower mass-specific RMR than kokopu and thus, according to MTE, they should have a higher mass-specific population density, which would require a species identity term to explain differences in population density (i.e. the Case One model: density = log(µMASS) x species identity). If mass-specific RMR differences were responsible for the mass-specific density difference, then a model that additionally included species mass-specific log(µRMR) (i.e.; the Case Two model) would explain the same variation as the Case One model, but log(µMASS) and species identity effects would become redundant.

In the Case One model, where the effect of log(µRMR) was excluded, the minimal adequate model that explained variation in mudfish and kokopu population density included both the direct effects of log(µMASS) and species identity (Table 1). Log(µMASS) was significantly positively related to population biomass density (mass effect: $F_{1,61}$ = 46.11, P < 0.001), with a slope of 0.96, which did not differ significantly between species (species x

mass interaction: $F_{1,60}$ = 1.44, P = 0.24) (Figure 3a). However, the intercept for this relationship was significantly higher for mudfish populations (species effect: $F_{1,61}$ = 42.24, P < 0.001) (Figure 3a). Excluding species identity resulted in a 36 percent reduction in the model R^2 from 0.52 to 0.19, and a large 30.56 unit increase in AIC_c. Thus there were large differences in population biomass densities between mudfish and kokopu that could not be explained by fish mass (Figure 3a).

Table 1: Model selection results for the Case One model (i.e. excluding species RMR differences) and the Case Two model (i.e. incorporating species RMR differences) evaluating the physiological controls on mudfish and kokopu population biomass density. R^2 is the coefficient of determination, AIC_c is Akaike's information criterion corrected for small sample size and *w* is the Akaike weight for the models that were simplified (i.e. all non significant terms removed) from their corresponding full model. Log(µMASS) and log(µRMR) are the average mass and resting metabolic rates of individual fish in a population in g and mg O_2 g^{-1} h^{-1}, respectively. Species identity is a two level factor (banded kokopu or brown mudfish). An asterisk denotes an interaction between the preceeding factor and all subsequent variables in brackets.

Case	Full model	Simplified model	R^2	AIC_c	*w*
1	Species identity*(log[µMASS])	log(µMASS) + species identity	0.52	98.5	0.4
2	Species identity*(log[µMASS] + log[µRMR])	log(µRMR)	0.51	97.6	0.6

In the Case Two model, that included the effect of differences in mudfish and kokopu log(µRMR), the minimal adequate model that explained variation in mudfish and kokopu population density included only the single effect of log(µRMR) (Table 1). Log(µRMR) was significantly negatively related to population biomass density (mass effect: $F_{1,62}$ = 65.17, P < 0.001), with a slope of –3.07, which was identical for both species (mass x species interaction: $F_{1,60}$ = 0.069, P = 0.79) and had an R^2 of 0.51 (Figure 3b). In contrast to the Case One model, there were no significant differences in population biomass density between species when density was regressed with log(µRMR) (Figure 3a, b) (species effect: $F_{1,61}$ =

1.79, $P = 0.19$). Thus mudfish and kokopu population densities were similar when comparing populations with similar average individual metabolic rates, but not when comparing populations with similar sized fish (Figure 3a, b). In fact, removal of log(μMASS) and species identity terms reduced the total model R^2 by only 0.04 units and the model AIC_c by 5.63 units. Consequently, the variance explained by log(μRMR) in the final case two model was virtually identical to that explained by the combination of species identity and log(μMASS) in the Case One model (Table 1). As a result, both case one and two models had similar degrees of support as shown by similar R^2, AIC_c, and w (Table 1). Nevertheless, the Case Two model using only log(μRMR) was the most parsimonious, which explained over 50 percent of the variation in population biomass density in a single variable, and had a greater proportion of the Akaike weight total, giving it slightly more support than the case one model that excluded log(μRMR) (Table 1). Consequently, the differences in mass specific population density between mudfish and kokopu were explained by species mass-specific RMR differences.

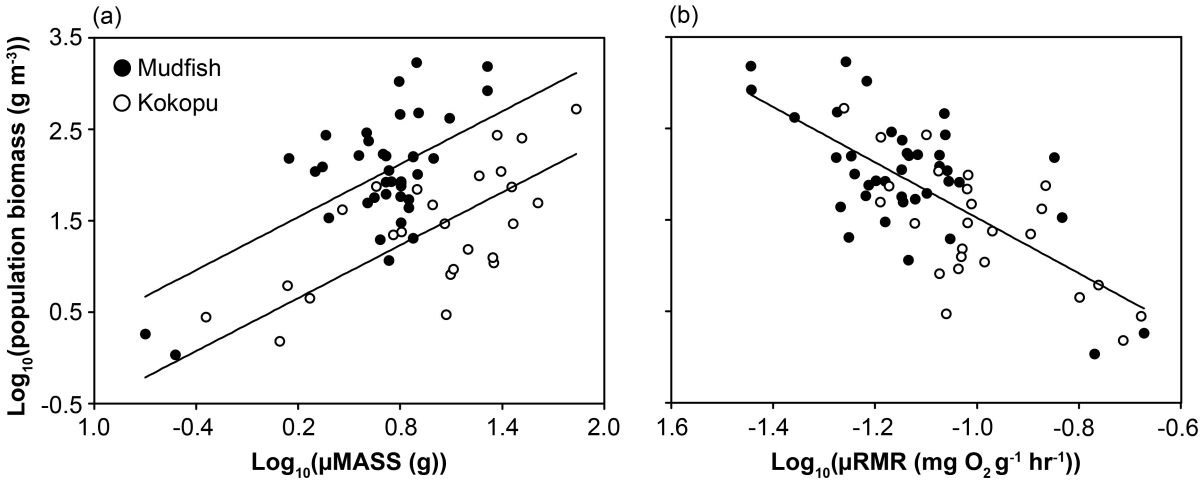


Figure 3: The effects of **(a)** the average mass of individuals in a population (log[μMASS]) in g and **(b)** the average resting metabolic rate (RMR) of individual fish in a population (log[μRMR]) in mg O_2 g^{-1} h^{-1}, on the density of biomass in mudfish (closed circles) and kokopu (open circles) populations. All data points are for individual populations, and all axes are log_{10} transformed. Slopes and intercepts were calculated from ANCOVAs after non-significant interaction terms in a homogeneity of slopes test were removed.

Discussion

Understanding how functional traits vary along environmental gradients will enhance predictions of species distribution and abundance at local ecological scales (McGill et al. 2006). I have shown how Habitat Templet theory (HTT) and Maximum Power theory (MPT) can be used as environmental templets to determine species metabolism along environmental gradients. This framework accurately predicted that low metabolic capacity would affect abiotic and biotic tolerance positively and negatively, respectively, in brown mudfish and banded kokopu. The a low metabolic capacity of brown mudfish (i.e. slow resting and maximum metabolic rates (RMR, MMR respectively), and low aerobic scope (AS)) likely explains why they are present in hypoxic, acidic and drought-prone pools, but are absent from benign pools where they are extirpated by more powerful kokopu. This pattern suggests an abiotic-biotic tolerance trade-off may be responsible for driving metabolic rate variation that

exists in many animals.

This framework accurately predicted that mudfish density would be higher for their mass because of their low mass-specific metabolic adaptation to physiologically stressful environments (Figure 4). Mudfish mass-specific population density was higher compared to that of kokopu for the range of fish sizes surveyed. This was because mass did not account for variation in species' mass-specific RMR. Consequently, differences in species intercepts for the relationship between mass and density (size-density relationship: SDR) disappeared when the species mass-specific RMR, which incorporated species identity and differences in metabolic rates, were used to predict density. Differences in habitat food production, which has been used to explain species density differences in the past (Carbone & Gittleman 2002), are unlikely to have caused mudfish and kokopu density differences because mudfish habitats were more physiologically stressful, which typically engenders lower, not higher, habitat productivity (Parsons 2005). Remarkably, log(μRMR) (i.e. the average consumption rates of fish in a population) explained 51 percent of the total variation in population biomass density, which was almost identical variation, explained by the combination of log(μMASS) (i.e. the average mass of fish in a population) and species identity (52 percent), which also suggests similar habitat productivity between species habitats. Thus mudfish and kokopu were functionally equivalent in density once their adaptation to abiotic and biotic stress tolerance was accounted for. This indicates that MTE can be locally relevant provided we understand how mass specific metabolic rates adapt species to local conditions.

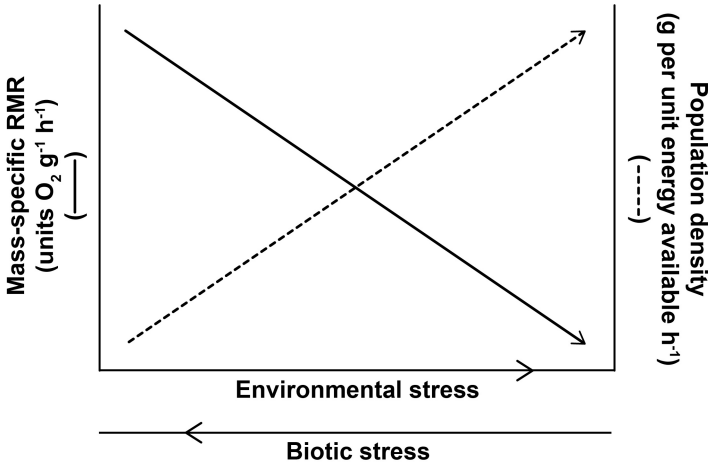


Figure 4: The predicted effects of an abiotic-biotic tolerance trade-off on fast versus slow metabolic adaptation, and the associated response of population density. Fast and slow resting metabolic rate (RMR) adaptation runs counter-current to biotic and abiotic stress respectively. High mass-specific metabolic rates are unsustainable in environmentally stressful habitats thus selecting for low RMR. However, low RMR is selected against as biotic stress increases in benign habitats because it hinders competitive or predator escape behaviours. The fast-slow continuum that this abiotic-biotic tolerance trade-off encourages results in relatively low and high population densities for abiotic and biotic stress tolerant species respectively (i.e. relative to species mass and energy produced over time in respective habitats), because of the changes in per-capita consumption rates that results.

Ideally, metabolic scaling exponents should be useful for predicting the slopes of SDRs (Brown et al. 2004). There were, however, large differences between the slope of the mudfish and kokopu SDRs and that predicted from their metabolic scaling relationships. Population biomass increased with log(µMASS) with a slope of 0.96 for both mudfish and kokopu, which is a higher rate than predicted from mudfish and kokopu mass-specific metabolic scaling relationships (a slope deviance of 0.63) (Brown et al. 2004). Such deviations could occur if food availability was greater for larger individuals (Begon, Firbank & Wall 1986; Blackburn & Gaston 1999; Steingrímsson & Grant 1999). For example, carrying capacity (C) would increase if both energy (E) increased and per unit consumption rate (P_c) decreased according to the equation: $C = E / P_c$ (Begon, Firbank & Wall 1986).

Because food availability was unlikely to have varied systematically with log(μMASS) across my sites, this result may have occurred due to the reduced gape limitation with increasing body size that occurs in animals (King 2002). I observed prey in my pools ranging from small amphipods (<5 mm long), through to moderately sized odonates and large terrestrially-derived *Prionoplus reticularis* beetle adults (New Zealand's largest terrestrial beetle) (Reid et al. 2011), thus providing a large range of prey sizes which would be made available during ontogeny. Moreover, I observed evidence of intense cannibalism, particularly amongst mudfish, which would provide additional food access as cohorts grew, such as has been suggested for other SDRs (Latto 1994). Thus the expectation of constant SDR exponents that are consistent with metabolic scaling relationships may be unrealistic (Carbone & Pettorelli 2009). Using mass-independent metabolic rate as a predictor of density avoids confounding allometric factors, such as gape size, and may therefore be a better way of testing the fundamental effects of metabolic variation on density as embodied in the MTE.

The opposing way in which low metabolic capacity affects abiotic and biotic stress tolerance implies species with low metabolic capacity will have large differences in their fundamental and realised niches. Low metabolic rates confer tolerance to a wide variety of physiological stressors such as drought, hypoxia, cold/freezing temperatures and low habitat productivity, which are all ultimately forms of energy stress, preventing the replenishment, or use of, ATP, through mechanisms which are universal to all species (Hochachka 1986; Hochachka 1988; Guppy & Withers 1999). However, low RMR often impairs competitive or anti-predator behaviour, which could make species sensitive to displacement by more powerful species (DeLong 2008; Biro & Stamps 2010). Thus low metabolic capacity may be a common trait that increases species fundamental niche because of increased co-tolerance to multiple environmental stressors, but simultaneously reduces species realised niche through decreased tolerance to biotic stress (Southwood 1988). This may explain why species

invested strongly in physiological stress tolerance, such as mudfish, often have large fundamental-realised niche ratios.

Habitat templet theory, which provides a framework for addressing the abiotic-biotic tolerance trade-off, predicts an increase in life-history plasticity from species adapted to constant physiological stress (*A*-selected species) to those adapted to periodic disturbance stress (*r*-selected species) (Southwood 1988) (Figure 1a). Although mudfish populations experience disturbance (drought), when there is water present, it is nearly fully anoxic and highly acidic, thus the difference in stress magnitude during and after disturbance is low (i.e. hypoxia is relatively constant over time). Moreover, rainfall in New Zealand is notoriously unpredictable making dramatic metabolic state shifts difficult to time (Winterbourn, Rounick & Cowie 1981; Winterbourn 1997), which may select for traits that prime species for both during and post-disturbance periods (i.e. adaptation for the average condition). Aerobic scope describes a species' ability to engage in fitness enhancing activities (predation and escape, growth and reproduction) (Killen et al. 2007), and hence may be a suitable correlate of such life history plasticity (Figure 1a, b). The low AS in mudfish compared to that of kokopu therefore supports the prediction that mudfish are adapted to the consistent presence of environmental stress, and may have low life-history plasticity (i.e. *A*-selected) (Figure 1a, b). Low metabolic rates improve tolerance to both droughts and hypoxia, thus a low RMR would be adaptive in hypoxic stable periods and would prime mudfish for unpredictable drought periods (Hochachka 1986; Hochachka 1988; Guppy & Withers 1999). This is in contrast with species inhabiting North American temporary pools, where seasonal droughts are highly predictable thus allowing for the timing of active growth periods, and either amphibious or sedentary stages during droughts, thus allowing for flexible, *r*-selected, life-histories (Welborn, Skelly & Werner 1996). Consequently, the relative difference in stress magnitude during stable and unstable periods, and the predictability of disturbances, may affect the

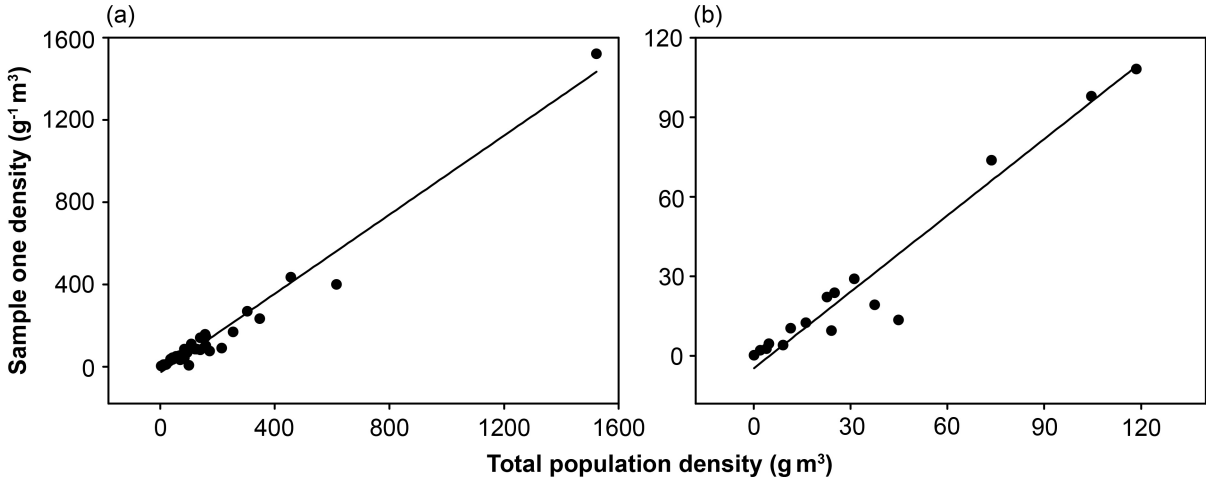
degree of metabolic plasticity, and hence abiotic stress tolerance in some species (Southwood 1988; Lytle & Poff 2004).

It is difficult to consider whether kokopu are either *r*- or *K*-selected based on their aerobic scope alone, as it is likely that both selection strategies would evolve higher aerobic scope (Figure 1b). For instance, higher aerobic scope would enhance predatory and foraging capacity as well as growth and reproduction (Killen *et al.* 2007; Killen, Atkinson & Glazier 2010), which is expected for competition-intense *K*-strategists (Southwood 1988). Instead, *r*- and *K*-strategists may be distinguished by their ability to metabolically depress (Figure 1b). For instance kokopu populations experience both normoxia (flowing water) and moderate hypoxia (McDowall 2006) thus providing selective pressure to either metabolically depress or have high aerobic scope. Meanwhile, North American drought-prone pond species either metamorphose to escape drought (thus avoiding the need to metabolically depress), or utilise drought-resistant egg stages (i.e. they undertake metabolic depression via egg diapause) (Welborn, Skelly & Werner 1996). Thus metabolic depression or aerobic scope may be equally viable traits for *r*-selected strategists. *A*-selected strategists, however, do not experience disturbance, and hence experience low selective pressure for metabolic depression, but are instead selected for intense competition and biotic stress (Southwood 1988), which may be enhanced by a high aerobic scope.

Overall, the functional traits-on-gradients framework involving MTE, HTT and MPT I have used has enhanced prediction of distribution and abundance in several ways that provide some generally useful insights. Firstly, by understanding the fundamental abiotic-biotic tolerance trade-off in terms of a fast-slow metabolic continuum, I was able to explain differences in mudfish and kokopu fundamental and realised niche and thus their distribution along abiotic contours. My data suggests low metabolic capacity positively and negatively affected mudfish abiotic and biotic stress tolerance respectively, thus explaining why mudfish

have a large fundamental niche but are extirpated from much of this by more powerful fish such as banded kokopu (i.e. large fundamental-realised niche ratio). This implies species mass-specific RMR may be a generally useful trait to predict species realised distribution along abiotic stress contours because it considers both abiotic and biotic elements that determine fundamental and realised niche respectively. Secondly, this framework allowed me to locally adapt MTE by accurately predicting that mudfish performance (i.e. density) would be higher for their size in environmentally stressful habitats because of their low mass-specific metabolic adaptation to physiologically stressful environments. Metabolic theory asserts that mmetabolic rates are the DNA of ecology, ultimately predicting that all species are equal in function when compared on a gradient of metabolic rates (Sibly, Brown & Kodric-Brown 2012). I have shown that kokopu and mudfish population densities were equivalent once their fast-slow mass-specific metabolic adaptation to local environmental conditions was accounted for (i.e. densities were compared to mass-specific RMR, not mass). Consequently, species metabolic adaptation to environmental conditions explained the local ecological contingency caused by intrinsic species traits and local habitats, thus allowing fundamental macro-ecological scale predictions of metabolic theory to be locally relevant.

Appendices



Appendix 1: For **(a)** mudfish and **(b)** kokopu, the relationship between the total population density (unique fish biomass from sample one + sample two) and the population density caught on the first sample. Both slopes are 0.95.

Chapter Four

General discussion: Implications for freshwater management in the context of global environmental change

Species distribution and abundance (D&A) is determined by both environmental gradients and intrinsic species traits (McGill et al. 2006). Human mediated environmental change is currently altering this fabric upon which D&A is determined by shifting abiotic gradients and introducing exotic species with new traits (Vitousek *et al.* 1997; Foley *et al.* 2005; Didham *et al.* 2007). Understanding how functional traits link species to their performance (i.e. population density) in different environmental contexts, will therefore be important for predicting how species D & A will be altered by changing environmental contexts (McGill et al. 2006).

I used the metabolic rates of brown mudfish (*Neochanna apoda*) and banded kokopu (*Galaxias fasciatus*) to understand how their distribution and abundance differed in alternative environmental contexts. Metabolic rates are useful predictors of species D&A because they reflect both the scope of an animals investment into fitness enhancing activities (e.g. growth, reproduction, foraging, predation), and how this scope is altered by abiotic conditions (Brown *et al.* 2004; Sibly, Brown & Kodric-Brown 2012). I combined three important ecological theories: the Metabolic Theory of Ecology (MTE) and Habitat Templet (HTT) and Maximum Power (MPT) theories (Lotka 1922; Southwood 1988; Brown *et al.* 2004), in order to predict how fish metabolism will affect their D&A in different environmental contexts. The metabolic theory of ecology predicts species population abundance will negatively correlate with their resting metabolic rate (RMR) because of the reduction in division of available energy between individuals of a population (Brown et al. 2004). Meanwhile, HTT and MPT theories hypothesise that fast metabolic rates will be

adaptive in benign environments, where species richness, and therefore competition, tends to be higher, but slow metabolic rates will be adaptive in physiological stressful environments where high metabolic rates are unsustainable (Lotka 1922; Southwood 1977; Greenslade 1983; Odum 1983; Southwood 1988). Thus HTT and MPT predict a trade-off between abiotic and biotic tolerance controlled by a fast versus slow metabolic rate trade-off, which determines species fundamental and realised niches respectively, and hence distribution. Consequently, HTT and MPT explain how fast versus slow metabolic rates will determine species distribution, while MTE explains how these metabolic rates will affect their abundance within this distribution (Lotka 1922; Southwood 1988; Brown *et al.* 2004).

The trade-off between abiotic and biotic tolerance predicted by habitat templet theory was well demonstrated by the contrasting distribution between mudfish and kokopu in Chapter Two. I showed how the realised niche of brown mudfish was a severely contracted portion of its fundamental niche, because of the presence of banded kokopu in benign pools, and was comprised of highly stressful abiotic elements, including extreme hypoxia, acidity and droughts. Banded kokopu predation in benign pools appeared to be responsible for this contracted realised niche of mudfish. Thus the relative distribution of mudfish and kokopu was driven by an abiotic-biotic tolerance trade-off as predicted by HTT and MPT (Lotka 1922; Southwood 1988). The incredibly high physiological tolerance of mudfish equips them for a large fundamental niche because they can tolerate a wide range of physiological stress, however, this has been traded-off with poor biotic stress tolerance resulting in a large fundamental-realised niche ratio (Chapter Two).

This abiotic-biotic tolerance trade-off was accurately predicted by fast versus slow metabolic rates in kokopu and mudfish respectively, according to my metabolic interpretation of HTT and MPT theories (Chapter Three). Mudfish had a significantly lower metabolic capacity in terms of resting metabolic rate (RMR), maximum metabolic rate (MMR), and

aerobic scope (AS) compared to kokopu (Chapter Three). The hypoxic, acidic, drought-prone pools mudfish are restricted to, essentially create a state of energy stress for mudfish by impairing oxidative phosphorylation due to hypoxia, by preventing foraging during drought, or placing energetic pressure on ionoregulation in low pH (Hochachka 1986; Bond, Lake & Arthington 2008; Glover, Donovan & Hill 2012). These pressures mean energy must be saved by reducing oxygen consumption so as to avoid inefficient energy use involving anaerobic metabolism (Hochachka 1986). Because many physiological stressors can ultimately be regarded as placing premiums on energy availability, or use (Southwood 1988), the low metabolic capacity of mudfish (Chapter Three) explains why they are tolerant to such a wide range of physiologically stressors, and hence why they have such a large fundamental niche (Chapter Two). However, because such metabolic depressions take energy away from fitness enhancing functions (i.e. growth and reproductive rates, predatory behaviour and foraging capacity), low metabolic capacities result in reduced biotic stress tolerance (DeLong 2008; Biro & Stamps 2010). Thus the low metabolic capacity of mudfish (Chapter Three) explains why they were absent from benign pools containing kokopu, and hence their restricted realised niche, and thus their high fundamental-realised niche ratio (Chapter Two).

Accordingly, the fast-slow metabolic trade-off embodied by HTT and MPT accurately predicted that mudfish performance (i.e. density) would be higher for their size because of their low mass-specific metabolic adaptation to physiologically stressful environments (Chapter Three). Metabolic theory asserts that metabolic rates are essentially the ‘DNA’ of ecology, ultimately predicting that all species are equal in function when compared on a gradient of metabolic rates (Brown *et al.* 2004; Sibly, Brown & Kodric-Brown 2012). My findings supported this claim by showing that mudfish and kokopu population densities were equivalent once their mass-specific metabolic differences were accounted for (Chapter Three). Consequently, species metabolic adaptation to environmental conditions explained

the local ecological contingency caused by intrinsic species traits and local habitats, thus making fundamental macro-ecological scale predictions from metabolic theory locally relevant. This emphasises the fundamental importance of metabolism in driving the D&A of mudfish and kokopu. Importantly, it shows that the restriction of mudfish to extreme physical conditions is not detrimental to the performance of their populations. Ultimately, this finding indicates that ecological function at the level of the population is invariant of species identity despite selection for trait differences at the individual level.

The finding that mass-specific RMR was negatively correlated with fish tolerance to physiological stress in mudfish and kokopu (Chapters Two and Three) may be a consistent pattern for freshwater fish in general, and certainly many New Zealand native freshwater fish. Figure 1 shows the negative relationship between the average abiotic stress of a species' habitat, and species mass-specific RMR (for five gram fish), for native and introduced freshwater fish in New Zealand. Abiotic stress in Figure 1 is calculated as the product of the average habitat pH and DO as determined from multiple surveys of fish distribution on the West Coast of the South Island, New Zealand, (including this one) from several authors (Greig et al. (2010) and O'Brien and Dunn (2007) and references therein; Chapter Two). It is, therefore, an estimate of species realised abiotic niche. This value is inversed such that higher values represent increased physiological stress (i.e. low pH and DO). Consequently, Figure 1 shows that species tend to occur in more physiologically stressful habitats as their RMR decreases.

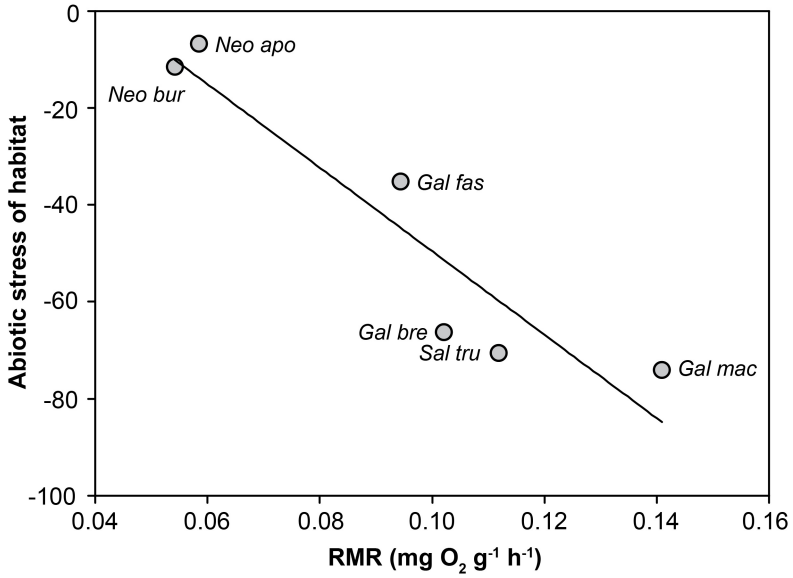


Figure 1: The significant negative relationship between mass-specific resting metabolic rate (RMR; at 10 – 15 °C and approximately 5 g) and the average habitat abiotic stress (the inverse product of the average habitat dissolved oxygen and pH: more negative = more benign) for six freshwater fish native to New Zealand (R^2 = 0.87, $F^{1,4}$ = 27.15, P = 0.006). Data sources for habitat conditions include Greig et al. (2010) and O'Brien and Dunn (2007) (and references therein), and Chapter Two (this thesis). Resting metabolic rates for *Neo bur* (*Neochanna burrowsius*), *Gal bre* (*Galaxias brevipinnis*), and *Gal mac* (*Galaxias maculatus*) were sourced from Meredith (1985), which were measured at 15 °C from fish of average mass 5.59, 4.78, and 5.59 g respectively. *Neochanna apoda* (*Neo apo*) and *Galaxias fasciatus* (*Gal fas*), RMRs are from Chapter Two (this thesis) measured at 14 °C. Brown trout (*Sal tru*) RMR was estimated for 5.3 g from the mass-RMR scaling relationship calculated by Bokma (2004) based on measurements made at 10 °C.

This ability to predict abiotic characteristics of species habitats from their RMR (Figure 1) will be useful for animal conservation for several reasons. Firstly, it implies that a single, relatively easy-to-measure, physiological metric, can be used to predict species actual distribution along abiotic gradients with relatively high accuracy (R^2 = 0.87). Furthermore, this RMR-stress relationship implies that the physiological controls of RMR on population density embodied in the MTE (Chapter Three) may extend to other species across abiotic gradients (Brown et al. 2004). This could drastically reduce the economic and time

investment that would otherwise be required to survey fish distribution and abundance in the wild to create a predictive model. Moreover, it provides the basis of an *a-priori* hypothesis for how species will respond to environmental change. For example, the introduction of brown trout (*Salmo trutta*) is predicted to negatively impact species with similar or lower RMR, particularly koaro (*Galaxias brevipinnis*) perhaps by displacing them into less optimal, more stressful conditions at the boundaries of their tolerance. This is precisely what has happened to some populations of Canterbury galaxias (*Galaxias vulgaris*), which have a similar RMR to koaro (Meredith 1985), and have been displaced into warmer, hypoxic, drought-prone reaches of streams in New Zealand, which brown trout cannot tolerate (Leprieur et al. 2006; McIntosh et al. 2010). Brown trout have had similar effects on native *Galaxias olidus* populations in Australian rivers (Closs & Lake 1996). Meanwhile, streams with low pH are important refuges from trout competition for galaxiids in West Coast streams of New Zealand's South Island (Olsson et al. 2006). Thus the RMR of introduced species may be used to predict their environmental impacts when other ecological information on such species is lacking.

The RMR-abiotic stress relationship also implies that a human-induced shift to either more environmentally benign or stressful conditions will negatively impact species with low or high RMR, respectively (Figure 1). In the case of brown mudfish, clearance of podocarp swamp-forests and conversion into pasture has reduced the amount habitat that is hypoxic, acidic or drought-prone, resulting in benign permanent drainage ditches, which are more habitable by other fish (McDowall 2006) (Figure 1, Chapter Two). Likewise, almost all of the original native habitat of the closely related endangered Canterbury mudfish (*Neochanna burrowsius*) has been lost due to wetland and forest conversion into pasture (McDowall & Eldon 1996; McDowall 2006). Drought-prone habitats are important for allowing the co-existence of Canterbury mudfish with native freshwater eels, and exclude other native and

introduced fish, which otherwise extirpate mudfish in more benign freshwaters (O'Brien 2005; Harding, Norton & McIntosh 2007). Meanwhile, the high metabolic rate of invasive *Gambusia affinis* (Mitz & Newman 1989) may prevent *Gambusia* establishment in drought-prone pool refuges of endangered black mudfish (*Neochanna diversus*), which otherwise negatively impact black mudfish populations in permanent marginal wetland habitats (Ling 2004; Ling & Willis 2005). As indicated by Chapter Two, mudfish are likely to be extirpated from such benign conditions by other fish. Thus, the low RMR mudfish species confirms mudfish populations as particularly vulnerable to the current regime of habitat degradation, which is shifting habitats towards a more benign state (Figure 1). Benign pools may arguably be less physiologically stressful, and therefore healthier for mudfish individuals (O'Brien & Dunn 2007). However, the high mudfish population densities in the extremely harsh pools (Chapter Three), combined with the refuge from predation that extreme conditions provide, creates a habitat of high mudfish biomass with significant conservation value. This implies that the dual influences of species introductions and land-use change towards a benign state in New Zealand may have a synergistic, negative effect on some native species, by shifting habitats towards conditions that favour invasive species (Didham et al. 2007). Consequently, preservation of existing swamp forests and wetlands should be a first priority for the long-term conservation of mudfish populations.

The finding that low RMR also increases a species' fundamental niche (Chapter Two, Three), nevertheless, suggests that there could be significant scope for conservation of stress tolerant taxa by translocation. Brown mudfish are physiologically un-restricted by abiotic conditions (excepting, perhaps, high velocity river flow), which mean there may be a large number of candidate lentic habitats for translocations, provided that dispersal barriers for other fish are provided. This could be particularly important, given that artificially creating the conditions of the mudfish realised niche (i.e. low oxygen: approximately 1.5 mg O_2 L^{-1};

low pH: <3.8; droughts), will be difficult given that they are formed by large scale podocarp swamp-forest dynamics. My research was conducted in Saltwater forest, an ancient podocarp swamp-forest remnant consisting of rimu (*Dacrydium cupressinum*) and kahikatea (*Dacrycarpus dacrydioides*) (Norton & Leathwick 1990; James & Norton 2002). Allocthonous detritus and terrestrial invertebrate input will be important for the formation of pool hypoxia and acidity (Ng, Tay & Lim 1994; Beamish, Beamish & Lim 2003) and provides energy for mudfish consumption. Meanwhile, pool drying is enhanced by pool shape, such that shallower pools dry more frequently than deeper pools. Such pools are naturally created by falling trees within the forest and as such likely require old growth temperate rainforest (Adams & Norton 1991). An example of such dynamics can be seen in the recent tornado disturbance that, in 2011, uplifted thousands of podocarp trees in Saltwater forest along an approximately five km line, thus creating thousands of potential new habitats for mudfish sub-populations. Consequently, passive mudfish conservation by conserving existing podocarp swamp forest dynamics will be highly effective, but active conservation should capitalise on the large mudfish fundamental niche using translocations, making use of artificial dispersal barriers to replace the natural barriers provided by habitat harshness. This may be particularly important for Canterbury mudfish, which have almost no natural wetland habitat left to conserve (McDowall & Eldon 1996).

The conversion of wetlands and swamp-forests into agricultural systems is a global issue (Brinson & Malvárez 2002; Giam *et al.* 2012). Such conversions are predicted to more than double the number of global freshwater fish extinctions by targeting extremophiles with restricted realised niches made up of harsh conditions (i.e. hypoxia, acidity, and drought), that are created by wetland swamp forests (Giam et al. 2012). My thesis suggests species extinction risk will be determined by their investment in abiotic or biotic stress tolerance and the direction of environmental change towards environmentally benign or harsh conditions. I

have shown how this sensitivity is determined by an abiotic-biotic tolerance trade-off mediated by fast or slow metabolic rates. Thus species with slow metabolic rates will be sensitive to extinction by a change towards more benign conditions, and the introduction of species with high metabolic rates and biotic stress tolerance. The use of species metabolic rates, therefore, provides a powerful potential tool with which to predict future environmental impacts on freshwater fish.

Glossary

AS	Factorial aerobic scope is the range of metabolic rates a fish is capable of, estimated as the ratio of the maximum and resting oxygen consumption rate for individual fish.
***A*-selected**	A slow paced life-history strategy proposed by Habitat Templet Theory for species adapted to constant abiotic stress, that have low growth rates and reproductive outputs and long lives.
C	Maximum carrying capacity for a population of fish (number of individuals or total biomass per unit habitat volume).
D & A	Distribution and abundance.
DO	Dissolved oxygen in mg O_2 L^{-1}.
E	Amount of energy available to a population of fish, produced per unit time and volume of habitat.
ETR	Emergent tree roots: Percentage of pool circumference with visible extruding tree roots.
HTT	Habitat Templet Theory of life-history strategies for species living in habitats differing in environmental and biotic stress.
***K*-selected**	An intermediately paced life-history strategy proposed by Habitat Templet Theory for species adapted to benign environments with high competition and predation stress. Species intermediate rates of growth and fecundity and intermediate life-length.
Log(µMASS)	The $\log_{10}$ of the average mass of individuals in a population of fish. An estimate of P_c given that resting metabolic rates are positively correlated with individual mass.
Log(µRMR)	The $\log_{10}$ of the average resting metabolic rate of individuals in a population of fish. An estimate of P_c.
MMR	Maximum metabolic rate of individual fish, estimated as the rate of oxygen consumption of individuals after exhaustive exercise.
MPT	Maximum Power Theory of natural selection for individuals that are the most efficient at converting energy into biomass within the constraints of their environment.
MTE	The Metabolic Theory of Ecology that uses the relationship between individual mass and resting metabolic rates to predict ecological phenomena such as maximum population density.
OHC	Overhead canopy cover: Percentage of sky covered by tree foliage.

OHV	Overhanging vegetation: Presence or absence of plants that overhang the pool circumference by >30 cm.
P_c	Per capita energy consumption within a population of fish. The average amount of energy consumed by individuals within a population per unit time, estimated from individual resting metabolic rates.
RMR	The metabolic rate of individual fish at rest in a post-absorptive state.
***r*-selected**	A dynamic life-history strategy proposed by Habitat Templet Theory for species adapted to temporary abiotic stress, that have short lives and variable, but rapid rates of fecundity and individual growth.
SDR	The relationship between the $\log_{10}$ of the average mass of individuals in a population of fish and the density of individuals or biomass in a population.
SWD	Submerged woody debris: The number of wood pieces within a pool that is at least 30cm L by 2.5 cm W.
SWF	Saltwater Forest in Westland National Park, South Island, New Zealand.

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